Dispersal, Survivorship, and Host Selection of *Culex erythrothorax* (Diptera: Culicidae) Associated with a Constructed Wetland in Southern California

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ABSTRACT Three mark-recapture studies were carried out at a constructed wetlands facility in San Jacinto, CA, to examine the dispersal and population ecology of the most abundant host-seeking mosquito, Culex erythrothorax Dyar, collected in carbon dioxide-baited traps. Recapture rates were 0.3, 7.4, and 13.9% for August, September, and October, respectively. The mean distance traveled per night was \approx 0.5 km, and females were not recaptured farther than 2 km from the release site. Most marked individuals (\geq 99.5%) were recaptured within 0.5 km of the release point. Marked individuals were recaptured for 33 d after release. Horizontal estimates of survival calculated using recapture data were 0.89, 0.87, and 0.84/d for August, September, and October, respectively. Temporal differences in the recapture rate were attributed to the effects of blood meal acquisition on host-seeking activity versus effects of mortality and strong developmental site fidelity on weekly recapture rates. Partially engorged females collected by CO₂-baited traps at the wetland fed predominantly on cattle indicating that host-seeking females were using hosts at dairies surrounding the wetland and were returning to the wetland for resting before seeking an additional blood meal. Estimates of the gonotrophic cycle length and survivorship (vertical estimates) were problematical because of the low parity rates for females collected by CO2-baited traps. Limited dispersal and long survival of Cx. eruthrothorax are important factors in the development of large populations at constructed wetlands.

KEY WORDS *Culex erythrothorax*, constructed wetlands, dispersal, survivorship, host selection, mark-recapture

IN RECIONS SUCH as southern California where human populations are growing rapidly, water usage and wastewater treatment are important concerns of urban planners and public health/environmental agencies (McCarthy 1997). Constructed wetlands designed to treat secondary effluent provide a functional equivalent of advanced (i.e., tertiary) wastewater treatment and are expected to play an increasing role in water reclamation strategies in arid regions of the United States (USBR, NBS and EMWD 1994, Mc-Carthy 1997). Treatment wetlands >10 ha are likely to be built in agricultural areas because of land availability and favorable costs; however, human development will inevitably encroach on large treatment wetlands as agricultural operations are replaced by urban and suburban sprawl. Wetlands are also added as esthetic amenities to urban and suburban developments. The proximity of artificial wetlands and human residences potentially poses significant public health and abatement problems from disease-transmitting and pestiferous mosquitoes.

Populations of *Culex erythrothorax* Dyar are often associated with thickly vegetated freshwater marshes in the western United States (Nielsen and Rees 1961, Chapman 1962, Bohart and Washino 1978, Jakob et al. 1989, Walton et al. 1998). Larval developmental sites include freshwater impoundments, seeps, and ditches that contain stands of tule (*Schoenoplectus* { = *Scirpus*} spp.) and cattail (Typha spp.) (Chapman 1962, Bohart and Washino 1978, Mian et al. 1990), vegetated river margins (Walters and Smith 1980, Jakob et al. 1989), and large permanent swamps (Nielsen and Rees 1961). Nutrient-rich water and a climate favorable for nearly year-round growth caused vegetation to proliferate rapidly in a constructed wetland in southern California during the 3 yr after wastewater treatment was initiated (Thullen et al. 1999). Cx. eruthrothorax host-seeking populations in the summer increased concomitantly at a rate of an order of magnitude per year, reaching a maximum of 33,000 females per CO₂baited suction trap night (Walton et al. 1998).

Culex erythrothorax is an important pest of humans (Chapman 1962) and of domestic animals (Reisen and Reeves 1990) because of opportunistic biting habits; however, dispersal of *Cx. erythrothorax* has not been studied in detail, particularly from artificial wetlands designed for water reclamation. *Cx. erythrothorax* exhibits crepuscular peaks in biting activity similar to those found in other *Culex* species (Cope et al. 1986, Cope and Hazelrigg 1989) but will bite readily during the day, if disturbed at resting sites in vegetation

J. Med. Entomol. 36(1): 30-40 (1999)

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within and surrounding freshwater wetlands. Although arboviruses have been isolated from *Cx. erythrothorax* (Emmons et al. 1974, Jakob et al. 1989), vector competence studies indicate that *Cx. erythrothorax* does not play an important role in arbovirus transmission in the western United States (Meyer et al. 1988, Reisen et al. 1992b). Evidence to date indicates that this mosquito does not disperse far from developmental sites (Dow et al. 1965, Walters and Smith 1980). Chapman (1962) suggested that *Cx. erythrothorax* could become a serious pest if its developmental sites were situated adjacent to areas inhabited by humans.

The purpose of the current study was to describe dispersal and the population attributes of survivorship, parity, and host selection of adult *Cx. erythrothorax* associated with a constructed wetland in southern California. Mark-release-recapture methodology was used to estimate the dispersal rates and to estimate survivorship of *Cx. erythrothorax* during the summer and autumn 1995. Parity status was used to estimate gonotrophic cycle length and to calculate vertical survivorship estimates. The factors contributing to the maintenance of large host-seeking populations and the movement of *Cx. erythrothorax* adults into the region surrounding a constructed wetland are discussed.

Materials and Methods

Study Area. Mark-release-recapture studies were carried out in August, September and October 1995 at a constructed, multipurpose wetland research facility in San Jacinto, CA, located ≈35 km southeast of Riverside. The site consisted of eight 0.1-ha experimental wetlands (research cells), two 0.2-ha wetlands (nursery cells for vegetation propagation), two 0.03-ha saline marshes, and a large 10-ha wetland. The research and nursery cells were in the 3rd yr of operation and contained dense stands of either Schoenoplectus californicus (Meyer) Soják or a mixture of S. californicus and S. acutus (Muhl. ex. Bigel.) Löve and Löve, respectively. The 10-ha wetland was located ≈ 0.4 km northwest of the research cell complex. The wetland was in the 1st yr of operation and, in contrast to wetlands in the research cell complex, was vegetated sparsely with the 2 bulrush species. The wetlands received secondary-treated sewage from Eastern Municipal Water District's Hemet-San Jacinto Regional Wastewater Treatment Facility located ≈0.75 km east of the wetland research complex. The area surrounding the wetlands and water treatment facility contained a mixture of sprinkler-irrigated agriculture (e.g., fodder such as alfalfa, grasses, corn), livestock operations (e.g., feedlot dairy operations, egg-laying poultry operations), and seasonally flooded wetlands used for waterfowl hunting.

Collecting, Marking, and Releasing Females. Hostseeking females were collected in dry-ice baited (≈ 1.5 kg CO₂ per trap) suction traps operated from ≈ 1500 hours until $\approx 45-60$ min before sunrise. A plastic collection chamber (volume: 4 liters) was attached below the fan housing of the trap by a collecting sleeve. At collection, the mosquitoes alighting on the netting



Fig. 1. Map of San Jacinto/Viejo showing the placement of CO_2 -baited traps used for the mark-release-recapture studies during 1995. Insert illustrates the 0.1-km contour (traps 23–26), the research cell complex, and the release point.

were driven into the collection chamber by carefully collapsing the sleeve. Mosquitoes were counted in the collection chambers using a modification of the strip method (Dow et al. 1965) and then dusted with release-specific colored fluorescent dusts (Radiant Color, Richmond, CA). Species composition was determined by identifying individuals collected in 2 traps.

In August, 1 group of mosquitoes was released just after dawn and a 2nd group was returned to the laboratory, counted, and released in the late afternoon at 1530 hours. The mosquitoes used in September and October mark-recapture studies were released immediately after marking in the morning. An afternoon release also was carried out in October. In this release, mosquitoes were enumerated and marked in the morning, but were maintained under subdued light in an air-conditioned laboratory near the release site until being released at 1530 hours. The release point was at the center of the research cell complex (Fig. 1).

Mosquitoes dispersing from the experimental marsh complex were recaptured by 20 (August) or 26 (September and October) CO_2 -baited traps arranged in a circular array using the release point as the origin (Fig. 1). Five traps were positioned on each of the 0.5, 1.0, 1.5, and 2.0 km contours from the release point. In September and October, 4 additional traps were

placed on the 0.1-km contour, and 2 traps were positioned at 3 km NE from the release point, to detect downwind dispersal aided by prevailing southwesterly winds during late afternoon and early evening. Traps were run on 2 consecutive nights in August (1–3 August) and 3 consecutive nights in September (12-15 September). Because marked individuals from the larger release in early September were collected in routine monitoring samples during September, traps were run consecutively for 5 nights in October (10-15 October). Captured mosquitoes were euthanized with carbon dioxide, returned to the laboratory, and counted. Marked individuals were identified using either incandescent lighting at 25-50× under a dissecting microscope (August) or a longwave (wavelength \approx 365 nm) UV light box (September and October).

Except for the weeks encompassing the September and October mark-recapture studies, 2 CO_2 -baited traps (operated without lights) were run weekly from \approx 1500 until 0830 hours from August until mid-December at 2 locations: the release point and \approx 0.4 km northwest of the release point at the perimeter of the 10-ha wetland. Mosquitoes were euthanized with carbon dioxide, returned to the laboratory, and marked individuals were identified under UV illumination.

Estimating Dispersal and Survival. Mean daily dispersal rates were corrected for the decrease in trap density with increasing distance from the release point using the method of Brenner et al. (1984). Horizontal survivorship was estimated using the regression method described in Milby and Reisen (1989). To account for sampling the marked population without replacement, the number of individuals recaptured was multiplied by a correction factor, CF, where

$$CF = P_0 / (P_0 - \sum_{1}^{r} \rho_x),$$

where P_0 is the number of individuals released and ρ is number recaptured on each day (x) from day 1 to end of recapture chain, t. The average recapture rate (per trap) for the 4 traps adjacent to the release point was calculated for the first 3 and 5 d after release in September and October, respectively, and for marked individuals from the September release that were recaptured during the October study.

The ovarian tracheation method (Detinova 1962) was used to determine parity weekly for 50–120 hostseeking females collected in the routine monitoring traps. Ovarian tracheation also was examined in marked individuals recaptured by carbon dioxidebaited traps. The length of the gonotrophic cycle was estimated by iteratively solving the equation (Davidson 1954)

$$s = \sqrt[g]{(\text{parous/total})}$$

until the vertical estimate of survivorship approximated the horizontal estimate from the regression method (Milby and Reisen 1989). In the above equation, the gth root of the proportion of parous females in the population provided a vertical estimate of survivorship (*s*) and *g* is the duration of the gonotrophic cycle. Dispersal can cause horizontal estimates of daily survival to be less than vertical estimates of daily survival (Reisen and Lothrop 1995). We assumed that losses due to emigration would be minimal because New Jersey light trap collections made throughout the region (H. Murray, Riverside County Health Department, unpublished data) and carbon dioxide-baited trap collections made in the current study indicated that *Cx. erythrothorax* was localized at the wetlands complex.

Meteorological Parameters. During each study, temperature, relative humidity, wind speed, wind direction, and barometric pressure were recorded at 30-min intervals at the water treatment plant located ≈ 0.75 km northeast of the release point. A weather station (model: Weather Monitor II, Davis Instruments, Hayward, CA) also was positioned ≈ 0.2 km southeast of the release site during the September and October studies. Wind speed (average and maximum wind speed), wind direction on a 16 direction scale (e.g., N, NNE, NE), air temperature, relative humidity, and barometric pressure were recorded continuously (5-s sampling intervals) and averaged for 1-min intervals.

Host Selection. Host selection patterns were determined for blood fed females collected by CO_2 -baited traps. The abdomen was removed from each female, placed into an individual gelatin capsule and frozen until analysis using the precipitin assay (Tempelis and Lofy 1963). Blood meals were tested against nonspecific mammal and bird antisera. Specific antisera used to test for potential mammalian hosts included bovines, feline, canine/coyote, rabbit, horse, squirrel, porcupine, and human. Antisera of passeriform and columbiform birds also were tested when a blood meal reacted with the nonspecific avian antisera.

Results

Dispersal and Direction of Movement. August Release. In August, the average daily maximum and minimum temperatures were 41.7 and 23.3°C, respectively, relative humidity ranged from 16 to 58%, and winds at dusk were northwesterly on day 1 and southwesterly on day 2. Wind speeds declined after dusk and remained comparatively low (<0.5 m/s) during the night.

On 1 August, 5,072 marked *Cx. erythrothorax* were released. At the time of the release, winds were calm in the morning but strong southwesterly and northwesterly winds (2-3 m/s) occurred in the afternoon. The recapture rate was low (0.3%) during the August study. Only 2 individuals were recaptured in a trap 2 km northeast (trap 16) of the release point on the 1st night after the release. Thereafter, all individuals (n = 17) were recaptured within 0.5 km of the release point. The predominant direction of movement during the 2nd night was southeasterly; the largest catches in traps outside the release point were in traps 2 and 3 (Fig. 1). The mean distance traveled was 2 km for day 1 and 0.5 km for day 2. When the data are weighted by



Fig. 2. Mean distance at recapture (km) per day for *Cx. erythrothorax* females during the September 1995 mark-recapture study. Predominant direction of movement during each 24-h period is indicated by an abbreviation above each bar in the histogram (N = north, NNE = north-northeast, and so on).

the number of individuals recaptured, the mean distance traveled during the August study was ≈ 0.6 km per night.

The last marked individual from this study was recaptured 25 d after release. Seven or more days after the release, marked individuals were not collected outside the research cell complex (≤ 0.1 km).

September Study. Average daily maximum and minimum temperatures from 12 September through 15 were 43.6 and 16.1°C, respectively, relative humidity ranged from 11 to 80%, and daily strong afternoon breezes dissipated after sunset. The winds at dusk on day 1 were northwesterly with an average velocity between 2–3 m/s. Southerly winds blowing at 1–2 m/s occurred at dusk on day 2 and dissipated during the 2 h after sunset. On day 3, southeasterly breezes between 0.6 and 1.6 m/s were blowing at dusk. After dusk on 14 September wind direction was variable; wind speed declined and remained comparatively low (<0.5 m/s) during the night.

Approximately 15,000 marked Cx. erythrothorax were released on the morning of 12 September. The recapture rate (7.4% of 14,956) in September was higher than during the August study. The mean distance traveled increased from 0.29 km per night for the 1st night after release to 0.62 km per night for the 3rd night after the release (Fig. 2), giving a rate of dispersal of 0.17 km per night. Individuals were recaptured in weekly monitoring samples at 0.4 km from the release point until 5 October. Thereafter, all individuals were recaptured within 0.1 km of the release point. The majority of females (99.7% = 1,111) was recaptured within 0.5 km of the release point. For females (n = 86) recaptured at ≥ 0.5 km from the release point, 86% was collected in trap 2 and 3. The last individual was recaptured 33 d after release on 14 October.

The distribution of unmarked individuals in traps outside the research complex was similar to that for the marked individuals. The majority of unmarked females (98.6%) was collected within 0.5 km of the release point. Of the unmarked individuals collected \geq 0.5 km from the release point, 73% was collected in traps 2 and 3 located 0.5 km S and E of the release point. However, unmarked individuals also were captured in traps >0.5 km north and east of the research cell complex: traps 10, 11 and 16. No marked individuals were collected in the traps at >1 km north and east of the release site.

October Study. In October, the average daily maximum and minimum temperatures were 34.4 and 10°C, respectively, and relative humidity ranged from 13 to 99% with daily maximum and minimum reflecting ocean (i.e., lower daily maximum air temperatures, higher relative humidity) versus desert influence (i.e., higher daily maximum air temperatures, lower relative humidity) on the weather patterns. Wind conditions differed during the morning and afternoon releases of individuals marked with release-specific colored fluorescent dusts. At the time that marked individuals were released in the morning on 9 October winds were calm. Strong westerly breezes (2.7-3.1 m/s) occurred when marked individuals were released in the afternoon and brisk westerly breezes (1.2-2.4 m/s) continued until dusk on 9 October. Winds shifted from the south to the west and northwest at dusk on 10 October. Winds at dusk were predominantly westerly on 12 October. Winds were out of the south at dusk on 11 October and 13. On 11 October and 13, wind speeds at sunset varied from 1 to 2.4 m/s and 1.2-1.7 m/s, respectively. Wind speeds typically declined after dusk and remained comparatively low during the night.

Approximately 25,000 marked Cx. erythrothorax were released in October. The weighted average for percent recaptures in the October studies was 13.9%, and most females (99.5%) were recaptured within 0.5 km of the release point. The mean distance traveled increased at a rate of 0.09 km per night from 0.42 km per night on the 1st night after release to 0.7 km per night for the 4th night after release (Fig. 3A). The mean distance at recapture declined on the 5th night after release. The maximum distance at recapture was 2 km; 2 individuals were collected northeast of the release site, in trap 16, on the 4th night after release. Individuals were recaptured in weekly monitoring samples at 0.4 km from the release point until 2 November. The last individual was recaptured at the release point at 32 d after release on 9 November. A small proportion of the recaptures (0.002) was marked with 2 dusts (i.e., from the September and October studies), indicating long-term survival.

The mean distance traveled for mosquitoes released in the afternoon did not differ appreciably from that for mosquitoes released in the morning. One individual from the afternoon release was recaptured at 1 km from the release point on the 2nd night after release. All other marked individuals (n = 158) were recaptured within 0.5 km of the release point. For mosquitoes released in the afternoon, the mean distance traveled for nights 1–5 was greatest on the 2nd night after release (Fig. 3B). The mean distance traveled was greatest on the 4th night after release for individuals released in the morning. However, the greatest mean



Fig. 3. Dispersal characteristics of *Cx. erythrothorax* females during the October 1995 mark-recapture study. (A) The mean distance traveled (km) per day by females marked with 2 florescent dusts during the Ocotber 1995 study. Distances are corrected for trapping effort and weighted by the number of females released at 2 times of day. Predominant direction of movement during each 24 h period is indicated by an abbreviation above each bar in the histogram (N = north, NNE = north-northeast, on so on). (B) The mean distance traveled by females released in the morning (solid bars) and females released in the afternoon (open bars) during the 5 d after release in October 1995.

distance traveled for both groups was similar: 0.73 km for the group released in the morning and 0.70 km for the group released in the afternoon. Eleven mosquitoes released in the morning were recaptured at 1 km from the release point. Two individuals were recaptured at 1.5 (traps 11 and 14) and 2 km (trap 16) from the research cell complex. The remaining recaptures (n = 3,315) were made within 0.5 km of the release point. The recapture rate of 6.3% for the 2,504 marked females released on the afternoon of 9 October was <50% of that for the order of magnitude larger group (recapture rate = 14.3%; number of marked females = 22,376) released in the morning.

The predominant direction of movement of *Cx.* erythrothorax (marked and unmarked females) from the wetlands in October was within a quadrant with a radius equal to 2 km and extending from north to east of the center of research cell complex. The largest trap catches outside the research cell complex (i.e., >0.1-km contour) were in traps 1, 2, and 3 at 0.5 km from the release point. For locations >0.5 km from the release point, traps 7, 10, 11, and 16 collected greater numbers of host-seeking females than did the other traps. Traps at distances >0.5 km to the south and southeast of the research cell complex rarely contained *Cx. erythrothorax*. Host-seeking female *Cx. erythrothorax* were not collected in traps 17, 21, and 22 located east and northeast of the research cells.

Horizontal Survival Estimation. The number of females recaptured declined at a constant rate during each mark-recapture study (Fig. 4A). The relationship between the ln-transformed number of recaptures versus time was linear (Table 1). For regressions fitted to all of the recapture data for each study, the probability of daily survival was estimated to be 0.90, 0.88, and 0.87 for August, September, and October, respectively. Although, the relationship of recaptures versus



Fig. 4. The number of marked *Cx. erythrothorax* females recaptured in carbon dioxide-baited traps operated on consecutive nights during the 1st wk of 3 mark-recapture studies and during weekly monitoring in 1995. (A) The number of females recaptured and linear regressions calculated for the entire study. The best fitting regression lines for each study are illustrated. (B) The number of *Cx. erythrothorax* females recaptured plotted as a function of days after release. The best-fitting regressions are illustrated for the collections made during the 1st wk after release and for weekly monitoring samples. The open square is not included in regression data for August in both panels.

Study	Weeks	Slope $(\pm SE)$	Intercept $(\pm SE)$	F	Р	R^2	Survival(s)
			Entire study				
Aug.	1-5	-0.101(0.019)	3.179 (0.354)	28.95	< 0.013	0.906	0.899
Sept.	1-6	-0.117(0.013)	4.813 (0.268)	75.92	< 0.001	0.927	0.883
Oct.	1-6	-0.133(0.020)	5.249 (0.359)	43.73	< 0.001	0.846	0.867
			Split studies				
Aug.	2-5	-0.117(0.029)	3.550 (0.621)	15.78	0.058	0.89	0.89
Sept.	1	-0.710(0.351)	5.845(0.751)	3.975	0.295	0.799	0.290
Sept.	2-6	-0.133(0.014)	5.263 (0.366)	83.78	< 0.003	0.966	0.867
Oct.	1	-0.725(0.111)	6.836 (0.370)	5.26	< 0.008	0.934	0.275
Oct.	2-6	-0.161(0.012)	6.094 (0.295)	188.4	< 0.001	0.984	0.839

Table 1. Horizontal survival estimates for Cx. erythrothorax calculated using recapture data from 3 mark-recapture studies in San Jacinto, CA, during 1995

time appeared to be curvilinear and cubic polynomial regressions of ln-transformed number of recaptures versus days after release were significant for the September (F = 26.78; df = 3, 4; P = 0.007) and October (F = 13.74; df = 3, 6; P = 0.01) studies, the incremental improvement in the coefficient of determination (R^2) was not significant in both cases (F tests, P > 0.3).

The decline in recaptures during the 1st wk after release was more abrupt than for samples from the 2nd through the 5th wk after releases (Fig. 4B). Survival rates calculated for the period ≥ 10 d after release were 0.89, 0.87, and 0.84 females per day for August, September, and October, respectively. These survival rates were equivalent to those calculated using all of the recapture data for each study (Table 1). The recapture data for the August study were not considered further because recapture rates were markedly lower as compared to the later releases. The number (In-transformed) of recaptures during the 1st week after release was linearly related to time in September and October and the slopes (September: slope = -0.71 recaptures per day; October: slope = -0.73recaptures per day) of the 2 lines were approximately 6-fold larger than for the period ≥ 10 d after release in the September (-0.13 recaptures per day) and October (-0.16 recaptures per day) studies. If the survival data for daily samples during the 1st wk after release are considered separately from the period ≥ 10 d after release, the survival rates of adult females are unrealistically low: 0.29 and 0.28 d^{-1} for September and October, respectively. Although the same trend is evident during the 1st wk after release for both studies, the regression for September is not statistically significant (Table 1: F = 3.98; df = 1, 1; P > 0.05).

Survival from Analysis of Parity. Based on carbon dioxide-baited trap collections, 4 cohorts of mosquitoes occurred between the middle of July and the middle of November (Fig. 5). The number of hostseeking females ranged from 400 to 3,100 individuals per trap night during the summer. A peak in the population occurred in mid-October at 4,600 females per trap night. After the autumnal cohort declined in abundance, biweekly catches of the host-seeking population remained at ~1,200 individuals per trap night through the beginning of winter. Minima in catch size were separated by 4–5 wk.

Parity rates of unmarked females collected near the release point fluctuated in association with changes in the abundance of host-seeking females, but remained <0.3 (Fig. 5). For the period July through December, the mean for weekly estimates of the proportion of the population that was parous was 0.121 (SE = 0.063). Based on the proportion of the hostseeking population that was parous, the gonotrophic cycle of *Cx. erythrothorax* is estimated to have been 7.5–23 d (Table 2). The duration of the gonotrophic cycle was estimated to be >14, 13, and 8.5 d in August, September and October, respectively, using the maximum parity rates in 2 point running averages for each study. The vertically estimated probability of daily survival for the 3 cohorts were between 0.72 and 0.76 (Table 2).

Parity rates of marked females increased from $\approx 12\%$ during the 1st week after release to 93% by 3 wk after the release in October (Fig. 6). Parity rates of marked individuals were similar (11–14%) in samples collected during the 5 d following release. Nulliparous females were observed in all samples containing marked individuals. Only 3 marked individuals were collected in carbon dioxide-baited traps on 9 November; 1 female was still nulliparous at 33 d after release.



Fig. 5. Parity rates and the number of host-seeking *Cx.* erythrothorax females collected in routine monitoring samples using dry ice-baited traps at the research cell complex in San Jacinto, CA, for the period July through December 1995. The proportion parous females ($\diamond - \diamond$), a 2-point running average for parity status (-), and the number of host-seeking females collected per trap night (- -) are illustrated.

Study/cohort	Parity rate (P)		Gonotrophic cycle (days)		Survivorship	
·	Mean \pm SE	Max	P _{mean}	P _{max}	$P_{\rm mean}$	P _{max}
Study						
Aug.	0.068 ± 0.017	0.080	23^a	21^a	0.680^{b}	0.697^{b}
Sept.	0.132 ± 0.039	0.180	16^a	14^a	0.749^{b}	0.783^{b}
Oct.	0.134 ± 0.076	0.280	12.5^{a}	7.5^{a}	0.750^{b}	0.834^{b}
Cohort						
8 Aug.–14 Sept.	0.102 ± 0.046	0.163	7^b		0.722	
21 Sept15 Oct.	0.103 ± 0.051	0.180	7^b		0.723	
20 Oct15 Nov.	0.147 ± 0.075	0.280	7^b		0.760	

Table 2. Estimates of gonotrophic cycle length and survival of unmarked *Cx. erythrothorax* calculated using weekly mean and maximum parity rates for 3 mark-recapture studies and for 3 cohorts of adults from a constructed wetlands in San Jacinto, CA, in 1995

^{*a*} Assumes survivorship is equal to the horizontal estimates: August = 0.89, September = 0.88, October = 0.85.

^b Length of the gonotrophic cycle is assumed to equal 7 d.

Host Selection Patterns. Blood meals from 371 female *Cx. erythrothorax* were tested using the precipitin test; 92% fed on mammals and 8% for birds. Because most of the females contained small amounts of blood, the majority of blood meals was either too small or too digested for identification using the precipitin test. Only 72 (19.4%) blood meals were identifiable. Of the 66 individuals which fed on mammals, 54% fed on cattle, 28% fed on rabbits, and 1.5% fed on dog/coyote. Blood meals in the remainder (16.2%) reacted with serum reactive to mammals but not with any of the specific antisera. The 8% of females that fed on birds did not feed on passeriforms or columbiforms.

Discussion

This study showed that female *Cx. erythrothorax* disperse little, have an average probability of daily survival of ≥ 0.84 , and feed mainly on mammals. The limited dispersal and elongated persistence of adult female *Cx. erythrothorax* can result in large populations developing in the vicinity of constructed wetlands. The abundance of *Cx. erythrothorax* in CO₂-baited traps was generally an order of magnitude greater than the next most abundant species, *Cx. tar*-



Fig. 6. Parity rates of marked Cx. *erythrothorax* females recaptured during the October study in 1995. Numbers in parentheses are the number of females dissected to determine ovarian tracheation.

salis, at the study site (Walton and Workman 1997) and its midsummer abundance at the 10 ha demonstration wetland increased from \approx 200 females per trap night in 1995 to > 30,000 females per trap night in 1997 (Walton et al. 1999).

The daily mean distance traveled for Cx. erythrothorax averaged 1.5, 0.46, and 0.50 km per night for August, September and October, respectively. The overall mean distance moved nightly by females in our studies was 0.55 (SE = 0.44) km. The comparatively large value for August was the result of 2 individuals that were captured 2 km from the release point on the 1st night after the release. The mean distance traveled for the 2nd night of the August study was only 0.5 km per night. If the August data are weighted by the number of individuals recaptured, then the mean distance traveled during the August study was ≈ 0.6 km per night. On all other dates, the mean distance traveled ranged between 0.1 and 0.73 km per night. If individuals marked with different fluorescent dusts in the October study are treated as replicate daily samples, the mean distance traveled was between 0.22 and 0.44 km per night. A mean distance traveled equal to 2 km per night is therefore unusual for Cx. eruthrothorax and is probably the result of individuals that were caught in the strong prevailing winds during the afternoon release of mosquitoes in August. The afternoon release in October failed to confirm this hypothesis perhaps due to differences in wind speed and direction during the August and October releases.

The dispersion of the *Cx. erythrothorax* population was generally limited to sites <2 km from the developmental site. Females were recaptured close to the study site; most females ($\geq 99.5\%$) were recaptured within 0.5 km of the release point. The percentage recapture of *Cx. erythrothorax* near the release point was >15% larger than for a comparable sampling effort (within 1 km of the release point) of the more dispersive *Cx. tarsalis* (Reisen and Lothrop 1995). Only 4 marked *Cx. erythrothorax* were collected at 2 km NE of the release point and marked individuals were not collected in traps >2 km in the same general direction. The longest flights of females during the 1st night of the 3 studies were respectively 2, 1, and 1.5 km for August through October; however, the host-seeking population was localized with few host-seeking individuals moving >1.5 km from the constructed wetlands. Because unmarked *Cx. erythrothorax* females were rarely collected in traps farther than 1.0 km from the research cell complex and were never collected in CO_2 -baited traps at distances >2 km NE from the release point, an extended period of operation for traps in the concentric grid is unlikely to change the conclusion that *Cx. erythrothorax* populations remain comparatively localized.

The dispersal pattern of our San Jacinto mosquitoes was concordant with the limited dispersal tendencies of Cx. erythrothorax observed in previous studies. Walters and Smith (1980) found that Cx. erythrothorax dispersed short distances from a reed-salt cedar site along a river margin. Individuals were concentrated within 150 m from the developmental site and hostseeking females did not move farther than the bluffs bordering the floodplain (maximum distance across the floodplain: 0.54 km). The number of females collected by light traps on the river bank opposite the developmental site declined appreciably; the distance of the trap from the developmental site was only 180 m. Dow et al. (1965) observed that Cx. eruthrothorax remained localized compared with Cx. tarsalis; the maximum distance that a host-seeking individual moved was 2.4 km.

The distribution of potential hosts surrounding the wetland might influence the dispersal distance of Cx. eruthrothorax. Only 19% of the mosquitoes contained sufficient blood that could be identified in the test system used. The proportion of the San Jacinto population that fed on mammals (92%) is similar to that reported for *Cx. erythrothorax* populations in Orange and Los Angeles counties in southern California: San Joaquin Marsh, Orange County: 90.5% (Tempelis 1989); Orange and Los Angeles counties: 88% (Reisen et al. 1992b). Host selection patterns indicated that Cx. erythrothorax collected at the San Jacinto wetlands fed predominantly on cattle and to a lesser extent on rabbits. A concentration of potential hosts occurred at a dairy operation located ≈ 0.6 km south of the research cell complex. Host-seeking females rarely dispersed south farther than the dairy. Feedlot dairy operations are within 1 km on 3 sides (ENE, W, S) of the San Jacinto wetlands and probably limit the dispersal distances of *Cx. erythrothorax* into the surrounding region. The farthest dispersal by marked females was across fallow fields NNE of the release site. For situations where potential hosts are not as close to a developmental site or as concentrated as at San Jacinto, host-seeking females might disperse longer distances.

The limited dispersal tendencies and longevity of adult *Cx. erythrothorax* adult females were further evidenced by the persistent collection of marked individuals near the release point. Marked individuals were collected for 23–33 d after release. The abundance of marked individuals in routine monitoring samples declined exponentially beginning 1 wk after each release. Marked individuals were not recaptured at 0.4 km from the release site after 2 (August and October) or 3 wk (September). The fact that a small percentage of individuals (0.2%) carried colored dusts from a previous mark-recapture study indicates that adults are capable of living longer than 30 d in nature. All dual-labeled specimens (individuals marked with 2 colors of fluorescent dusts) were captured in traps on the 0.1 km contour indicating that during the period between studies either these individuals did not move beyond the research cell complex or individuals returned to the wetlands after blood-feeding in the surrounding region. Host selection studies found that partially engorged females collected by CO₂-baited traps at the wetland fed predominantly on cattle indicating that females were using hosts at dairies surrounding the wetland and were returning to the wetland for resting before seeking an additional blood meal. Based on the number of marked individuals in routine monitoring samples, the finite survival rates of Cx. erythrothorax females were 0.89, 0.87, and 0.84/d in August, September, and October, respectively, and are greater than the daily survival estimates for Cx. tarsalis and Cx. quinquefasciatus (Milby and Reisen 1989; Reisen et al. 1991, 1992a).

The net effect of outward dispersal from the release point on deletion processes is probably small relative to mortality for mosquito populations that exhibit site fidelity where individuals return to natal developmental sites for oviposition after host feeding. The slope of the ln-transformed number of recaptures versus time after release includes both death and emigration (Milby and Reisen 1989, Reisen et al. 1992a). For populations monitored over multiple gonotrophic cycles and for long-lived species such as Cx. erythrotho*rax* that show strong developmental site preferences, the emigration component of the horizontal survivorship method is likely to be a comparatively minor loss after 1 wk postrelease. If the data for >10 d after the release in the September and October studies represent the survival of a comparatively sedentary group of individuals (i.e., the decline in recaptures is caused primarily by mortality) and the survival rate is assumed to be constant for each study, then the data for recaptures during the 1st week after the release includes mortality and a comparatively larger 2nd component. The 2nd component will include factors that contribute to a decline in attractancy of carbon dioxide-baited traps to host seeking females such as (1) the portion of the population emigrating for blood meals and dispersing and (2) the portion of the population successfully obtaining a blood meal. If one assumes that the proportion of the population emigrating from the research cells is approximated by the proportion of individuals dispersing >1 km, then the emigration component is small ($\leq 0.05\%$) for Cx. erythrothorax. The resurgence of the number of recaptures in the 2nd wk after release indicates that marked individuals did not permanently disperse from the wetland developmental site. Conversion of the difference (Δs) between the slopes for the semilog plots of recaptures after day 10 versus time (i.e., weekly samples) and the recaptures before day 10 versus time (i.e., daily samples) to a finite rate of change provided an estimate of the proportional daily change in the 2nd component of population deletion factors. If the proportion of the population obtaining a blood meal per unit time is calculated as $e^{\Delta s}$, where *e* is the base of the natural logarithms, the proportion of the population successfully obtaining a blood meal during the 1st wk after release was similar for the September and October studies: 0.55 and 0.58/d, respectively. We conclude that the comparatively rapid decline in daily recaptures during the 1st wk after release was most likely caused by a decline in the attractancy of carbon dioxide-baited traps to marked females that have successfully obtained a blood meal.

Alternatively, temporal differences of recapture rates or mortality also might produce the differences in the relationship for recaptures versus time observed for *Cx. erythrothorax.* Recapture rates are known to vary temporally within a particular study when a cohort of newly-emerged adults is released. Age-related differences in dispersal (Gillies 1961) or factors which reduce the attractancy of traps to females such as active dispersal during the 1st few days after release (Navar et al. 1980) and additional time required for maturation and mating before host seeking (McHugh and Washino 1986) also might cause temporal variation in recapture rates. However, we released hostseeking females, so a delay in the onset of host-seeking was unlikely. Behavioral effects of sedentary versus agitated components of the marked population (Powell and Dobzhansky 1976) cannot be discounted.

Temporal differences of mortality rates are unlikely to have caused the striking differences observed in the regressions of recaptures versus time. The strong linear relationship for the semilog plot of recaptures per unit time for weekly samples indicates that mortality rate within each study is constant. For the October study when traps were run for 5 nights consecutively and then weekly thereafter, the number of individuals recaptured on day 10 was appreciably larger than the number of marked females collected on day 5. The number of individuals recaptured 3 d after release was similar to that at 10 d after release in September and October. The resurgence in the number of marked individuals captured in the 2nd week after release, the increase in the proportion of parous females in the marked population beginning 1 wk after release, and the strong linear relationship for recaptures per unit time support the hypothesis that the decline in recaptures during the 1st wk after release is indicative of successful host seeking by marked individuals and the increase in the number of marked, host-seeking females at 10 d after release is caused by individuals that are host seeking for the 2nd time.

Parity rates of unmarked *Cx. erythrothorax* were low (<0.3). Barr et al. (1986) found that the parity rate of *Cx. erythrothorax* attacking humans (0.25) was higher than that of females taken at traps baited with carbon dioxide (0.15) or birds (0.17). Parity rates of *Cx. erythrothorax* collected in June were higher (0.22–0.51) than for mosquitoes collected from July through September (range, 0.07–0.32) at the San Joaquin Marsh in Irvine, CA (Barr et al. 1986). Parity rates of the San

Jacinto mosquitoes collected by CO_2 -baited traps (range, 0.04–0.28) between July and December were very similar to those collected at Irvine; the average parity rate differed by only 5% (mean \pm SE for July– September: San Jacinto: 0.110 \pm 0.046; Irvine: 0.161 \pm 0.088). These parity rates are considerably lower than those reported for *Cx. erythrothorax* collected in 3 of 4 habitat categories within the Prado Basin, CA (Mian et al. 1990). Low parity rates indicate increased mosquito production or perhaps shorter longevity at the high ambient temperatures (Barr et al. 1986).

The low parity rates and the vertical estimates of survival are incongruous with the survival data for the marked populations at the San Jacinto wetlands. Vertical estimates of the gonotrophic cycle length based on parity status were unrealistically long with gonotrophic cycles of nearly 3 wk for data backcalculated using horizontal survivorship estimates. At more realistic gonotrophic cycles of 7 d, survival rates were only 0.68-0.78 females per day. Vertical estimates of survival calculated using parity data were thought to be more accurate than horizontal estimates of survival calculated using mark-recapture data because parity data do not include emigration (Milby and Reisen 1989). However, Aksnes and Ohman (1996) suggested recently that demographic studies using horizontal cohort analyses are more accurate than are vertical cohort studies where proportions in various stages of the life cycle are used to estimate mortality. Vertical estimation of survival from parity data requires several restrictive assumptions such as recruitment to the population must be constant and the population must have a stationary age distribution, age groups are sampled with equal probability, successive age groups can be identified accurately, transitions between age groups occur synchronously, and the time between age categories is relatively constant and can be estimated (Milby and Reisen 1989, Service 1993). Many of the aforementioned assumptions were not likely to be met by the Cx. erythrothorax population studied here. For example, changes in the parity rate and the population size indicate that recruitment was not constant and the age distribution was not stationary. Second, the parous portion in the population might have been undersampled by CO₂-baited traps (Barr et al. 1986). If the parity rate of the host-seeking population is assumed to be 0.25 (Barr et al. 1986), then gonotrophic cycle length was estimated to be between 8.5 and 12 d. Gonotrophic cycles of a week to 10 d in length were in closer agreement with recapture data, with parity data for marked individuals, and with the population dynamics of the host-seeking populations at the research cell complex than were gonotrophic cycles of 15-25 d. Additional studies are needed to determine the gonotrophic cycle length of Cx. erythrothorax; however, the gonotrophic cycle appears to be longer than for conspecifics studied by Reisen et al. (1992a).

We conclude that the predominant mosquito, *Cx.* erythrothorax, captured as host-seeking females in the vicinity of a constructed wetland research complex in southern California exhibits limited dispersal tendencies, has prolonged persistence, and feeds mainly on January 1999

mammals. The documented developmental site preferences of Cx. erythrothorax for tule marshes (Bohart and Washino 1978), a limited tendency of host-seeking females to disperse large distances from tule wetlands, and high survival of adults are important factors leading to large populations in the vicinity of wetlands. Some long distance dispersal is required to colonize new wetlands; however, our results suggest that long distance dispersal may be rare for the host-seeking component of the adult population. The development of large host-seeking populations and the propensity of this mosquito to feed on mammals (Tempelis 1989, Reisen and Reeves 1990, Reisen et al. 1992b, this study) and then return to wetlands after blood-feeding may create significant abatement concerns from host-seeking and meteorologically related displacements of pestiferous Cx. erythrothorax into regions of human habitation which are in propinguity to constructed wastewater treatment wetlands.

Acknowledgments

We thank A. Lagui, A. Luck, J. Liu, and M. C. Wirth for assistance processing the blood-fed mosquitoes. A. Caldwell (Capsugel) kindly provided gelatin capsules for blood-meal isolations. We benefitted from discussions with S. Denison, B. A. Mullens, W. C. Reeves, W. K. Reisen, and E. T. Schreiber. We thank M. Wirth and 2 reviewers for comments on this manuscript. We appreciate the cooperation of the U.S. Geological Survey, Eastern Municipal Water District, the U.S. Bureau of Reclamation and the Riverside County Department of Health. We thank Hugh Murray (Riverside County Department of Health) for lending equipment and the homeowners in San Jacinto who gave us permission to place traps on their properties. This work was supported by Special Funds for Mosquito Research from the Division of Agriculture and Natural Resources of the University of California, by U.S. Department of the Interior (National Biological Service) Cooperative Agreement No. 1445-CA09-0011, and by USDA funding to the Agricultural Experiment Station at UC-Riverside.

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Received for publication 15 October 1997; accepted 11 August 1998.