NATURAL VARIABILITY IN THE SEASONAL OCCURRENCE AND DENSITIES OF ADULT POPULATIONS OF OCHLEROTATUS SIERRENSIS

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ABSTRACT. This study examined the utility of Fay traps baited with carbon dioxide (Fay/CO₂ traps) and ovitraps for monitoring adult *Ochlerotatus sierrensis* over time and space in the Coast Range of northern California. During a 3-year study in a dense oak woodland, Fay/CO₂ traps collected adults from March to November at rates that were correlated with air temperature through peak activity periods ending in late June for males and late July for females. Variability in total annual rainfall did not explain the 3-fold difference in the numbers of females caught among years. Yearly collections were all male-biased, but sex ratios varied to the extent that early season densities of males did not reliably predict subsequent densities of females. Determinations of the seasonal activity periods of females by Fay/CO₂ traps and ovitraps were similar except that adults were captured 2–4 wk before oviposition occurred. The availability of natural oviposition size of females either among or within years. In a subsequent comparison of 3 sites, Fay/CO₂ trap captures of females lst peaked in mid-April at each location, but peak periods of host-seeking activity lasted 1, 7, and 18 wk in woodlands with open, moderate, and closed tree canopies, respectively. Significant differences in the densities of host-seeking females were not detected by the use of ovitraps because egg counts had similar magnitude and peaked between mid-May and mid-August at each location.

KEY WORDS Ochlerotatus sierrensis, host-seeking, oviposition, Fay/CO₂ trap, ovitrap

INTRODUCTION

Ochlerotatus sierrensis (Ludlow), the western tree hole mosquito, is widely distributed in lowerelevation woodlands of temperate western North America (Darsie and Ward 1981) and has a life cycle adapted to the Mediterranean climate (Hawley 1985). Females lay most of their eggs above water in tree holes after the end of the rainy season in spring (Woodward et al. 1998). Most of these habitats dry completely during the annual summer drought and the eggs do not hatch until rain fills the tree holes, usually during the wet months of fall and winter (Washburn et al. 1989). After development to the 4th instar, larvae enter diapause until long day length cues pupation in spring (Jordan and Bradshaw 1978). Adults of both sexes are attracted to hosts, primarily mammals, where mating occurs and females obtain blood meals (Washburn et al. 1992). Females often create a serious biting nuisance for humans (Garcia et al. 1989) and they are known to be important vectors of both Dirofilaria immitis (Leidy), the canine heartworm (Weinmann and Garcia 1974), and Setaria yehi (Rudolfi), the deer body worm (Lee 1971).

Accurate comparisons of adult population densities across time and space could be important for evaluating control measures directed against *Oc. sierrensis.* However, the adults are rarely collected in light traps (Lee 1971) and the most widely used alternative, the use of human sentinel collections (e.g., Lee 1971, Hawley 1985), is not often practical for long-term or widespread surveillance (Washburn et al. 1992). Among methods that have been previously tested for monitoring *Oc. sierren*- sis, the use of Fay traps (Fay and Prince 1970) baited with carbon dioxide (Garcia et al. 1989) (Fay/ CO₂ traps) offers the most promise as an economically feasible method for comparing populations over time and space. These traps are amenable to standardization, they capture adults of both sexes (Garcia et al. 1989), and they are reported to be a reliable measure of population density. For example, catches of females in Fay/CO2 traps were correlated both with catches in rabbit-baited traps (Garcia et al. 1989) and with collections made by human sentinels (Washburn et al. 1992). Ovitraps have also been used to monitor females, but their use primarily has been limited to studies of the distributions of oviposition (e.g., Woodward et al. 1996). Although this technique might also be amenable to standardization for multiple-year or multiple-site studies, any relationships between egg counts and female population size have not been determined. In this study, the utility of both traps was assessed during 3 years of activity in the same oak woodland. In a subsequent comparison across space, host-seeking and ovipositional activities were monitored in woodlands with open, moderate, and closed tree canopies (Mayer and Laudenslaver 1988) over the course of the same year. The objectives of these studies were to monitor variability in the seasonal occurrence and densities of adult Oc. sierrensis in northern California, to examine the relationships between Fay/CO₂ trap and ovitrap surveillance, and to assess the utility of each method for comparing adult populations over time and space.

MATERIALS AND METHODS

Three-year surveillance of a single site: The study was conducted during 1991, 1995, and 1996 in a dense northern oak woodland (Munz 1965) dominated by interior live oak (*Quercus wislizenii* Candolle) and Pacific madrone (*Arbutus menziessii* Pursh) near Potter Valley, Mendocino County, CA (39°14'N, 123°06'W). Polyethylene rulers were mounted in 10 water-filled tree holes that were located in the woodland (mean maximum depth \pm SD = 17.1 \pm 8.2 cm, range = 6.4–30.0 cm) and water depths were recorded weekly from mid-March to mid-November of each year. Daily precipitation and maximum air temperature data were obtained from a U.S. National Weather Service station at Potter Valley.

Two east-west transects (each ca. 100 m long) of the woodland were established for the placement of traps. Fay traps baited with 3.2 kg of dry ice (per Garcia et al. 1989) were hung from tree limbs and operated 1.25 m above ground at 1 station located near the center of each transect (ca. 40 m apart) for periods beginning at approximately 1400 h and ending at approximately 1000 h the next day. The traps were operated once per week from April 3 to November 18, 1991, March 25 to November 16, 1995, and April 16 to October 22, 1996. Live adults were anesthetized with carbon dioxide, identified ($10 \times$ magnification), and counted in the field and released. Dead adults were returned to the laboratory for identification and enumeration.

Each ovitrap (Woodward et al. 1996) consisted of a black plywood box (29 cm high, 15 cm wide, 18 cm deep) with a hinged lid and a screened (2.5cm mesh) vertical entrance (11×11 cm) near the top of the front panel that held a polyethylene cup (473 ml) lined with a Terri-wiper® towel strip (10 \times 27 cm), which was the oviposition substrate. Each cup held blue oak (Quercus douglasii Hooker and Arnott) tree hole water (380 ml) as an ovipositional attractant. All attractant water was collected from the same tree hole (ca. 85-liter volume), which was refilled with deionized water after each collection. Eight ovitraps were operated continuously at the same locations (4 on each transect) on the ground on the north sides of trees (>25 m apart) from April 3 to December 4, 1991, April 11 to December 11, 1995, and April 24 to November 19, 1996, with weekly replacement of the attractant water and ovitrap liners. All eggs of Oc. sierrensis oviposited onto the liners were identified and counted in the laboratory.

Single-year surveillance of 3 sites: During 1997, adults were monitored at the same Potter Valley site, a foothill woodland (Munz 1965) near Lakeport, Lake County, CA (39°01'N, 122°55'W) dominated by blue oak and California white oak (*Quercus lobata* Nee) and a blue oak-gray pine (*Pinus sabiniana* Douglas) woodland (Mayer and Laudenslayer 1988) near Lower Lake, also in Lake County, CA ($38^{\circ}54'N$, $122^{\circ}38'W$). Percent tree canopy closures (determined from averaging estimates in 1,600-m² blocks that included the trap transects in each woodland) were 82% at Potter Valley, 57% at Lakeport, and 29% at Lower Lake. Based on these percentages, the tree canopies at each habitat were classified (per Mayer and Laudenslayer 1988) as closed (>60%), moderate (40–59%), and open (25– 39%), respectively. Maximum air temperature data for the Lake County sites were obtained from a U.S. National Weather Service station in Lakeport.

Two Fay/CO₂ traps and 8 ovitraps were operated at Potter Valley in the same locations as in previous years. Two Fay/CO₂ traps and 6 ovitraps were operated along an east-west transect (ca. 130 m long) of the woodland at Lakeport. A north-south transect (ca. 110 m long) at Lower Lake was used to establish stations for 2 Fay/CO₂ traps and 5 ovitraps. The traps at each site were operated with similar methods and placement to those described for previous years at Potter Valley, except that the attractant water used in the ovitraps was 25% blue oak tree hole water and 75% blue oak leaf infusion. A single batch of attractant water was prepared for use at all 3 sites each week according to Woodward et al. (1996). The Fay/CO₂ traps were operated weekly at each site from March 4 to October 24. Ovitraps were operated continuously with weekly service from March 26 to December 1.

Statistical analyses: Statistical analyses conformed to Zar (1980). Methods used included Kruskal–Wallis analyses of variance followed by multiple range tests and Spearman rank order correlation analyses.

RESULTS AND DISCUSSION

Three-year surveillance of a single site

Rainfall and tree hole water depths: The 30-year mean (July 1–June 30, 1961–90) annual precipitation at Potter Valley was 112.9 cm, of which 97% fell between October 1 and May 31. Precipitation during the same months totaled 65.4 cm in 1990– 91, 170.1 cm in 1994–95, and 130.1 cm in 1995– 96. All 10 monitored tree holes held water during the wet winter months of each year, but in 1991 (Fig. 1A), every tree hole dried during spring. In 1995 (Fig. 2A) and 1996 (Fig. 3A), none of the tree holes dried until summer and the deepest tree holes retained water until late August and late September, respectively.

Seasonal occurrence of adult activity: Adults were caught in Fay/CO₂ traps from late April to early October in both 1991 (Fig. 1B) and 1996 (Fig. 3B) and from late March to early November in 1995 (Fig. 2B). A nearly complete overlap in the activity periods of both sexes occurred during each year.

The peak activity periods of adults shown in Figs. 1B, 2B, and 3B were similar, but delayed ap-

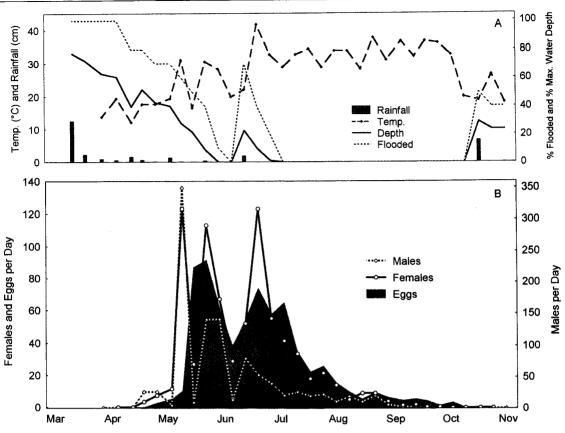


Fig. 1. Surveillance of the Potter Valley woodland in 1991. (A) Total weekly precipitation and maximum air temperature during Fay/CO₂ trap periods are scaled on the left. Percent of tree holes (n = 10) holding water and percent of mean maximum water depth (17.1 cm) are scaled on the right. (B) Mean numbers of adult Ochlerotatus sierrensis caught in 2 Fay/CO₂ traps and mean numbers of eggs oviposited into 8 ovitraps.

proximately 3 wk for each sex, when compared to emergence patterns reported for overwintering immatures within the area. In studies by Woodward et al. (1988) and Washburn et al. (1989), >75% of male emergence occurred during April, whereas a similar percentage of females emerged during a more prolonged period between mid-April and early June. The average date of male eclosion preceded that of females by 23 and 20 days in those studies, respectively. During the present study, 79% of male captures in Fay/CO2 traps occurred between April 24 and June 28, whereas 80% of females were caught during later and longer peaks in activity between May 7 and July 27. Yearly mean capture dates of females occurred 21-28 days after those of males. Intervals of 2-4 wk between emergence and female host-seeking activity have been reported previously for Oc. sierrensis (Lee 1971, Garcia 1975) and attributed both to a temperaturedependent development period that occurs after eclosion (Bennett 1978) and to weather that is too cool to stimulate host-seeking behavior (Lee 1971). In the present study, the magnitude of adult activity at Fay/CO₂ traps also was affected by temperature.

By combining seasonal data from all 3 years, capture rates were correlated with maximum air temperature through the peak activity periods ending June 28 for males (R = 0.63, P < 0.01) and July 27 for females (R = 0.71, P < 0.01). As temperatures increased and populations declined later in each season (Figs. 1–3), correlations of capture rates with air temperatures were not significant for either males (R = 0.28, P > 0.05 after June 28) or females (R = 0.27, P > 0.05 after July 27).

The low levels of activity observed for both adult sexes during late summer and fall (Figs. 1B, 2B, and 3B) also are consistent with emergence patterns known for *Oc. sierrensis*. For example, when utilizing the same Potter Valley study site, Garcia et al. (1989) found that annual emergence was 90% complete by the end of April for males and by early July for females, but some emergence continued into early August and early September for each sex, respectively. In addition, at a nearby study site, Washburn et al. (1989) found that some tree holes that retained water late into summer supported development of small 2nd cohorts of larval *Oc. sierrensis*. Although summer generation emergence ac-

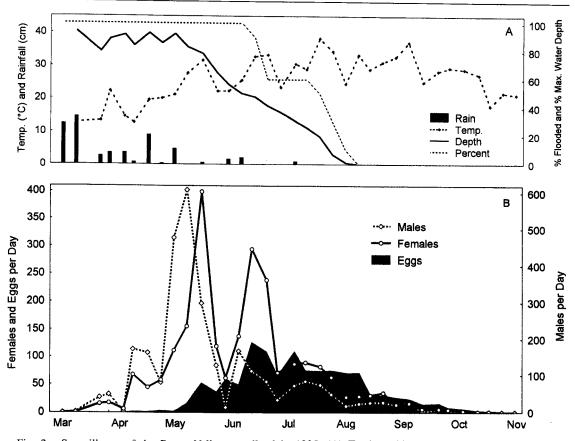


Fig. 2. Surveillance of the Potter Valley woodland in 1995. (A) Total weekly precipitation and maximum air temperature during Fay/CO₂ trap periods are scaled on the left. Percent of tree holes (n = 10) holding water and percent of mean maximum water depth (17.1 cm) are scaled on the right. (B) Mean numbers of adult *Ochlerotatus sierrensis* caught in 2 Fay/CO₂ traps and mean numbers of eggs oviposited into 8 ovitraps.

counted for less than 10% of total adult production from these tree holes, they produced a high proportion of males and added adults of both sexes to the late-season population.

In the present study, eggs of *Oc. sierrensis* were found in ovitraps 2 wk after the 1st collections of host-seeking females in both 1991 (Fig. 1B) and 1996 (Fig. 3B). The same interval lasted 4 wk in 1995 (Fig. 2B), but it coincided with colder weather that year. Oviposition subsequently occurred into October in 1991 and 1996, but in 1995, females laid eggs into the ovitraps from late April to early November. Most of the eggs (mean $\% \pm SD = 86.5 \pm 6.0\%$) were laid between mid-May and mid-August of each year. Phenologically, Figs. 1–3 show that these peak oviposition periods temporally overlapped the progressive decline in tree hole water depths that occurred after the onset of summer drought in each year.

Seasonal abundance of adults and eggs: Total Fay/CO₂ trap collections of adult *Oc. sierrensis* were male-biased each year (Table 1); however, these catches may not reflect actual sex ratios of the populations because females are attracted to the

traps during only a portion of each gonotrophic cycle (Garcia et al. 1989). Sex ratios among years also varied to the extent that the early season peak densities of males did not reliably predict the subsequent peak densities of females (Table 2). Variability in the densities of females among years also lacked correlation to annual rainfall or to tree hole water depths during the spring pupation period of overwintering immatures. For example, Table 2 shows densities of females were similar during the drought in 1991, when all of the tree holes dried during spring, and in 1996 when twice as much precipitation occurred.

Yearly ovitrap and Fay/CO₂ trap surveillance did not show a direct relationship between these 2 methods of monitoring female activity. For example, comparisons among years (Table 2) showed female densities were similar in 1991 and 1996, but 3 times more eggs were laid into the ovitraps during 1991. Berry et al. (1980) previously determined that competition from natural oviposition sites was an important factor affecting the numbers of eggs laid into ovitraps by female *Ochlerotatus triseriatus* (Say), the eastern tree hole mosquito. Among the

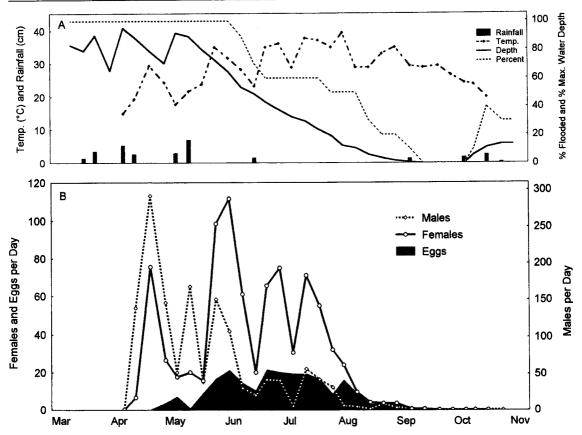


Fig. 3. Surveillance of the Potter Valley woodland in 1996. (A) Total weekly precipitation and maximum air temperature during Fay/CO₂ trap periods are scaled on the left. Percentage of tree holes (n = 10) holding water and percent of mean maximum water depth (17.1 cm) are scaled on the right. (B) Mean numbers of adult Ochlerotatus sierrensis caught in 2 Fay/CO₂ traps and mean numbers of eggs oviposited into 8 ovitraps.

10 natural tree holes monitored in the Potter Valley woodland (Figs. 1A, 2A, and 3A), the mean number that held water during the seasonal oviposition periods of females (Figs. 1B, 2B, and 3B) was significantly lower (Kruskal–Wallis analysis of variance, P < 0.01) during 1991 (mean = 1.72) than in either 1995 (mean = 4.55) or 1996 (mean = 6.74). Examination of these data suggests that a high ratio of eggs (per ovitrap day) to females (per Fay/CO₂ trap day) occurred in 1991 because females laid a larger proportion of their eggs into the ovitraps when the availability of natural oviposition sites was low.

A comparison of ovitrap and Fay/CO_2 trap results within years also failed to show a direct relation-

ship between the 2 methods of surveillance. Ratios of eggs to females showed a progressive month-tomonth increase during each year of the study (Fig. 4). Because host-seeking precedes oviposition, some increase in egg to female ratios was expected early in each season as nulliparous females began to seek hosts. For example, at a nearby study site, Lee (1971) found that 25% of host-seeking females collected during May were parous, whereas 93% or more were parous during each month from June through September. The relatively stable parity rates observed by Lee (1971) after May suggest that other factors had more importance in causing the progressively higher egg to female ratios shown for June through November in Fig. 4. After the on-

Table 1. Total collections of Ochlerotatus sierrensis during 3 years of surveillance at the Potter Valley woodland.

Life stage	Method of collection	Total number collected		
		1991	1995	1996
Males	Fay/CO ₂ traps	2,081	5,695	2,769
Females	Fay/CO ₂ traps	1,543	4,554	1,658
Eggs	Ovitraps	38,725	65,054	12,039

Life stage	Activity period	Mean number per trap day ³		
		1991	1995	1996
Males	April 24–June 28	78.65 a	221.40 b	114.35 ab
Females	May 07–July 27	56.92 a	151.63 b	51.04 a
Eggs	May 16–Aug. 16	44.95 a	65.06 a	14.24 b

Table 2.	Mean number of adults' and eggs ² of Ochlerotatus sierrensis collected in peak activity periods at the
_	Potter Valley woodland during 3 years of surveillance.

Adults were collected with 2 Fay/CO₂ traps operated once per week.

² Eggs were oviposited into 8 ovitraps operated with weekly trap periods.

³ Numbers in same row followed by different letters are significantly (P < 0.05) different by a Kruskal–Wallis analysis of variance followed by a multiple range test.

set of summer drought, the number of water-filled tree holes present in the woodland generally declined during each season (Figs. 1A, 2A, and 3A), suggesting the possibility of a relationship between the progressive decline in the availability of natural oviposition sites and the progressively higher egg to female ratios shown in Fig. 4. Regressing weekly data from the 1st oviposition of each year until all of the tree holes dried (1991 and 1995) or the last oviposition occurred (1996), ratios of eggs (per ovitrap day) to females (per Fay/CO₂ trap day) were negatively correlated (P < 0.01) with the percentage of natural tree holes holding water during each year of the study (Fig. 5). Examination of these data indicates that the availability of natural oviposition

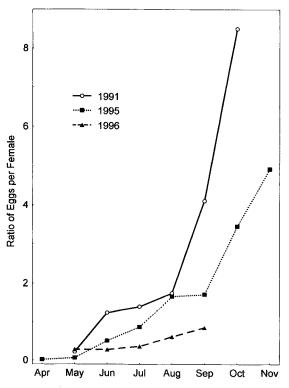


Fig. 4. Monthly ratios of eggs of *Ochlerotatus sierrensis* per ovitrap to females per Fay/CO₂ trap during 3 years of surveillance at the Potter Valley woodland.

sites was an important factor affecting ovipositional totals into the ovitraps and that females laid a larger proportion of their eggs into the ovitraps as natural tree holes dried over the course of each season.

Single-year surveillance of 3 sites

Seasonal occurrence of adults and eggs: Surveillance with Fay/CO₂ traps 1st detected peaks in activity by adult Oc. sierrensis in mid-April at each location, but the duration of the subsequent peak activity periods varied in relation to percent tree canopy closure at each site (Fig. 6). Catches of both sexes exceeded 20 adults per day for 17 of 18 weeks until mid-August in the closed canopy habitat. In the moderate canopy habitat, more than 20 adults per day of each sex were caught during a 7wk period ending in mid-May, but in the open canopy habitat, similar catches occurred only during April for periods of 2 wk for males and 1 wk for females. In similar respect to previous years at the closed canopy habitat, seasonal Fay/CO₂ trap catches of host-seeking females were correlated with air temperatures during a 17-wk period ending in late July (Spearman's R = 0.61, P < 0.01). At the moderate and closed canopy habitats, more than 50% of the seasonal Fay/CO₂ trap catches of females occurred during 4- and 1-wk periods, respectively. As a result, variability in air temperature was not a reliable long-term indicator of the densities of hostseeking females at either of those sites (Spearman's R < 0.13, P > 0.59 through July 27).

In contrast to Fay/CO₂ traps, ovitraps produced similar seasonal patterns of female activity regardless of percent tree canopy closure (Fig. 6). Oviposition 1st occurred in mid-April, with seasonal peaks between mid-May and mid-August at each location. Factors that caused the similar seasonal patterns of oviposition and disparate patterns of host-seeking activity among the sites were not determined with the methods used in this study; however, examination of the results of other studies suggests several avenues for future research. In a study of *Oc. triseriatus*, Beier et al. (1982) found that host-seeking females tended to aggregate in a small area of an Indiana woodlot that had dense cover, but some of them optimized use of limited

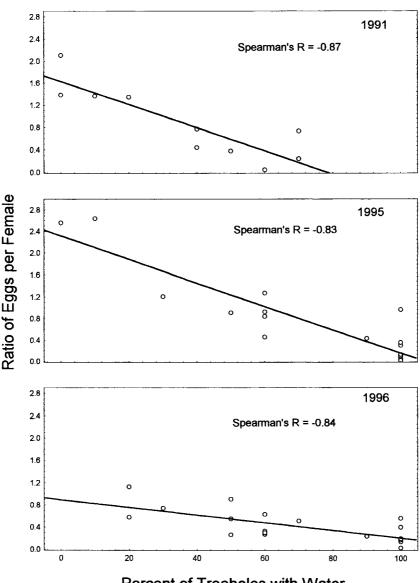




Fig. 5. Regression analysis comparing weekly ratios of eggs of *Ochlerotatus sierrensis* per ovitrap to females per Fay/CO₂ trap with the numbers of monitored tree holes (n = 10) holding water at the Potter Valley woodland. All weekly data are shown from the 1st oviposition of each year until all of the tree holes dried (1991 and 1995) or until the last oviposition occurred (1996).

tree hole resources for larval populations by distributing their eggs into other areas of the forest. Populations of *Oc. sierrensis* also are limited by the availability of nutrients for the larval stage (Colwell et al. 1995, Eisenberg et al. 2000) and because females prefer to occupy shaded areas to locate hosts (Lee 1971), water-filled tree holes located in open habitats would be underutilized as breeding sites unless some females searched these areas for oviposition sites. The habitat preferences and movements of female *Oc. sierrensis* that are seeking oviposition sites have not been determined, but examination of the results of the present study suggests that they were willing to utilize the open canopy habitat for oviposition even though very few of them used it to locate hosts.

Seasonal abundance of adults and eggs: Total Fay/CO₂ trap catches of adult *Oc. sierrensis* were greatest in the closed canopy habitat and decreased in relation to decreasing canopy closure at the other sites (Table 3). Sex ratios were highly male-biased within each habitat type. The Fay/CO₂ trap and ovitrap results were not consistent as a measure of the magnitude of female activity. For example, during

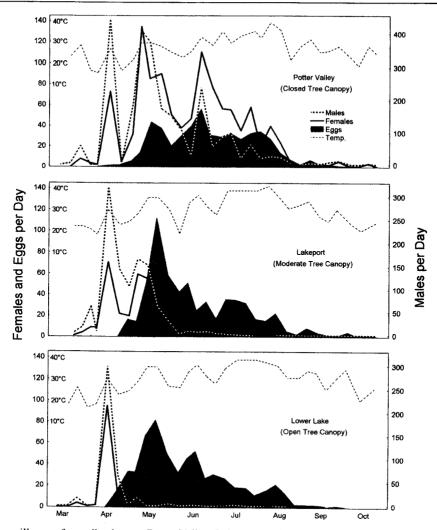


Fig. 6. Surveillance of woodlands near Potter Valley, Lakeport, and Lower Lake in 1997. Mean numbers of adult *Ochlerotatus sierrensis* caught in 2 Fay/CO₂ traps are shown for each location along with the mean numbers of eggs oviposited into 8 (Potter Valley), 6 (Lakeport), and 5 (Lower Lake) ovitraps. Maximum air temperature during each Fay/CO₂ trap period is scaled on the inside of each left y axis.

the mid-May to mid-August peak ovipositional period that occurred at each site, the mean numbers of eggs laid into the ovitraps were not significantly different, but the numbers of females collected in Fay/CO₂ traps varied more than 13-fold between sites (Table 4). Examination of these results shows that the number of eggs laid into ovitraps was not a useful parameter for comparing the densities of host-seeking females among the sites.

Implications for surveillance and control studies of Oc. sierrensis

The lack of a direct relationship between annual precipitation and the abundance of adults during the 3-year study at Potter Valley does not rule out the probability that these factors are likely to be correlated (e.g., Hawley 1985) over a longer time period or during years with more variability in rainfall. However, examination of the results does show that comparisons of adult density among small groups of years may include a fairly wide range of natural variability that is difficult to explain. This finding emphasizes the need for surveillance of control populations during field tests of possible control methods for this mosquito. Selection of multiple experimental sites should include consideration of the characteristics of each habitat. For example, differences in percent tree canopy closure among sites could introduce a natural source of variability in adult density (Fig. 6) that would complicate the comparison of treated and control areas. In addition, although air temperatures did not show a long-term correlation to adult densities in all types

Life stage	Method of collection	Total number collected		
		Potter Valley (closed canopy)	Lakeport (moderate canopy)	Lower Lake (open canopy)
Males	Fay/CO ₂ traps	5,242	2,247	837
Females	Fay/CO_2 traps	2,132	736	376
Eggs	Ovitraps	27,773	25,454	20,834

Table 3.	Total collections of Ochlerotatus sierrensis in northern California woodlands with closed, moderate, and
	open tree canopies during 1997.

of habitat, examination of the results indicates that fluctuations in adult density at some sites may be correlated to air temperature and this parameter should be considered when comparing populations over time or space.

The comparison of Fay/CO₂ traps and ovitraps showed that the former were more useful for monitoring populations of Oc. sierrensis over time or space. Their efficacy for measuring densities of host-seeking females was established previously (Garcia et al. 1989, Washburn et al. 1992). In this study, yearly Fay/CO₂ trap surveillance (Figs. 1B, 2B, and 3B) repeatedly showed patterns of activity by both sexes of adults that were consistent with emergence patterns of Oc. sierrensis (Woodward et al. 1988, Washburn et al. 1989, Garcia et al. 1989), indicating that these traps also can be used to assess seasonal variability in the densities of males. However, even though the protandrous emergence pattern of Oc. sierrensis was consistently evident in Fay/CO₂ trap catches at Potter Valley, examination of the results shows that it would be difficult to rely upon early season measurements of male activity as a means of anticipating the timing or magnitude of peak periods of host-seeking activity by females. The initial peaks in activity by each sex had little or no temporal separation at any of the sites monitored in this study (Figs. 1B, 2B, 3B, and 6). In addition, year-to-year variability in sex ratio was so high that early season densities of males were not a reliable indication of the subsequent densities of females (Table 2).

The numbers of eggs laid into ovitraps varied

Table 4. Mean numbers of females¹ and eggs² of *Ochlerotatus sierrensis* collected in woodlands near Potter Valley, Lakeport, and Lower Lake between May 12 and August 14, 1997.

	Mean number per trap day ³			
Life stage	Potter Valley	Lakeport	Lower Lake	
Females	58.88 a	12.18 b	4.36 b	
Eggs	32.46 a	38.79 a	35.57 a	

 $^{\rm t}$ Females were collected with 2 Fay/CO₂ traps operated weekly at each site.

² Eggs were oviposited into 8 (Potter Valley), 6 (Lakeport), and 5 (Lower Lake) ovitraps operated with weekly trap periods.

³ Numbers in the same row followed by different letters are significantly (P < 0.05) different by a Kruskal–Wallis analysis of variance followed by a multiple range test.

according to the availability of natural oviposition sites (Fig. 5), precluding their use as a direct measure of female population size either among or within years at particular locations. Based on this finding, ovitraps would not be a suitable tool for evaluating the effectiveness of a source reduction program for Oc. sierrensis. After the elimination of accessible water-filled tree holes from a woodland, females that emerged from inaccessible locations would encounter fewer natural oviposition sites and oviposition into ovitraps could increase even though the population size was reduced. When comparing data from different sites (Fig. 6), ovitrap results could not be relied upon to provide an indication of either the temporal occurrence or magnitude of peak periods of host-seeking activity by female Oc. sierrensis. As a tool for detecting the presence of Oc. sierrensis, ovitraps were insensitive to activity for a period of 2-4 wk after the 1st captures of host-seeking females, but ovitraps were at least as effective as Fay/CO₂ traps during the remainder of the season.

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REFERENCES CITED

- Beier JC, Berry WJ, Craig GB Jr. 1982. Horizontal distribution of adult Aedes triseriatus (Diptera:Culicidae) in relation to habitat structure, oviposition and other mosquito species. J Med Entomol 19:239-246.
- Bennett SR. 1978. Use of thermal summations to predict host-feeding rates of *Aedes sierrensis* in northern California. *Proc Pap Calif Mosq Vector Control Assoc* 46:46.
- Berry WJ, Fish D, Craig GB Jr. 1980. The use of an ovitrap grid for measuring adult movement and population density of the treehole mosquito *Aedes triseriatus*. *Proc Indiana Acad Sci* 89:208.
- Colwell AE, Woodward DL, Anderson NL. 1995. Environmental factors affecting the western treehole mosquito (Aedes sierrensis). Northwest Sci 69:151-161.
- Darsie RF Jr, Ward RA. 1981. Identification and geographical distribution of the mosquitoes of North America, north of Mexico Fresno, CA: American Mosquito Control Association.

Eisenberg JN, Washburn JO, Schreiber SJ. 2000. The gen-

eralist feeding behaviors of *Aedes sierrensis* larvae and their effects on protozoan populations. *Ecology* 81:921–935.

- Fay RW, Prince WH. 1970. A modified visual trap for Aedes aegypti. Mosq News 30:20-23.
- Garcia R, Colwell AE, Voigt WG, Woodward DL. 1989. Fay–Prince trap baited with CO₂ for monitoring adult abundance of *Aedes sierrensis* (Diptera:Culicidae). J Med Entomol 26:327–331.
- Garcia R, Des Rochers BS, Telford AD. 1975. Surveillance and detection of *Aedes sierrensis* (Ludlow). *Proc Pap Calif Mosq Vector Control Assoc* 43:156.
- Hawley WA. 1985. Population dynamics of Aedes sierrensis. In: Lounibos LP, Rey JR, Frank JH, eds. Ecology of mosquitoes: proceedings of a workshop Vero Beach, FL: Florida Medical Entomology Laboratory. p 167– 184.
- Jordan RG, Bradshaw WE. 1978. Geographic variation in the photoperiodic response of the western tree-hole mosquito, *Aedes sierrensis. Ann Entomol Soc Am* 71: 487-490.
- Lee DL. 1971. The role of the mosquito, *Aedes sierrensis*, in the epizootiology of the deer body worm, *Setaria yehi*. Ph.D. dissertation. University of California, Berkeley, CA.

Mayer KE, Laudenslayer WF Jr. 1988. A guide to wildlife

habitats of California Sacramento, CA: California Department of Fish and Game.

- Munz PA. 1965. A California flora Berkeley, CA: Univ. Calif. Press.
- Washburn JO, Anderson JR, Mercer DR. 1989. Emergence characteristics of *Aedes sierrensis* (Diptera:Culicidae) from California treeholes with particular reference to parasite loads. *J Med Entomol* 26:173–182.
- Washburn JO, Woodward DL, Colwell AE, Anderson JR. 1992. Correlation of *Aedes sierrensis* captures at human sentinels with CO₂-baited Fay–Prince and duplex cone traps. *J Am Mosq Control Assoc* 8:389–393.
- Weinmann CJ, Garcia R. 1974. Canine heartworm in California with observations on *Aedes sierrensis* as a potential vector. *Calif Vector Views* 21:45–50.
- Woodward DL, Colwell AE, Anderson NL. 1988. The aquatic insect communities of treeholes in northern California oak woodlands. *Bull Soc Vector Ecol* 13:221– 234.
- Woodward DL, Colwell AE, Anderson NL. 1996. Temporal and spatial distribution of Aedes sierrensis oviposition. Proc Pap Calif Mosq Vector Control Assoc 64:51–62.
- Woodward DL, Colwell AE, Anderson NL. 1998. Surveillance studies of Orthopodomyia signifera with comparisons to Aedes sierrensis. J Vector Ecol 23:136–148.
- Zar JH 1980. *Biostatistical analysis* Englewood Cliffs, NJ: Prentice-Hall, Inc.