

BIONOMICS AND VECTOR POTENTIAL OF *LEPTOCONOPS FOULKI* AND *L. KNOWLTONI* (DIPTERA: CERATOPOGONIDAE) IN THE LOWER DESERT OF SOUTHERN CALIFORNIA, USA

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Abstract. The bionomics of adults of the *Leptoconops kerteszi* complex were studied from March through October 1981 at the Salton Sea in southern California, USA. Miniature surveillance traps baited with dry ice were used to attract and capture host-seeking midges. Two species, *L. foulki* and *L. knowltoni*, were present from March-June and June-October, respectively. Both species readily imbibed nectar, and *L. knowltoni* was captured up to 2.8 km from the site of larval development; significantly more females were captured in ground-level traps than in traps at 2 m. Host-seeking activity was diurnally bimodal, with peaks just after sunrise and just before sunset. Differences between the magnitude of morning and afternoon peaks were attributed in part to differences in the age of the respective populations. Gonotrophic age-grading and observations on follicular maturation indicate that both species are anautogenous and that parous females seek hosts primarily in the afternoon, thus establishing a diel biting cycle. Parous rates varied from 0-81% in morning populations and from 37-39% in afternoon populations. Biparous females were seen in *L. knowltoni* populations in July-October. The vector potential of *L. foulki* peaked in May, with an average capture rate of 35.6 uniparous host-seeking females per hour. Vector potential of *L. knowltoni* peaked in August, with mean attack rates of 124.6 parous females per hour; 39.8 of these were biparous.

Leptoconops Skuse is 1 of 4 genera of hematophagous ceratopogonid midges (Kettle 1962, Linley et al. 1983). Members of this genus are widely distributed throughout the tropics and subtropics and are known for their vicious diurnal biting habits (Wirth 1952, Kettle & Linley 1967, Wirth & Atchley 1973). Certain species are known to affect tourism adversely on some Caribbean islands (Linley & Davies 1971) and have occasionally interrupted agricultural work in central and southern California (Wirth 1952, Steffen 1981).

Few studies have examined the biology of *Leptoconops* or their impact on the health of man and animals (Kettle 1965, Linley et al. 1983). Near the Salton Sea in southern California, Foulk (1969) studied diurnal flight activity, attack behavior, and

resting behavior of a species referred to as *L. kerteszi* [later designated as *L. knowltoni* by Clastrier & Wirth (1978)]. In southern California (Steffen 1981) and Japan (Kimura 1959), severe dermatitis has resulted from bites of *Leptoconops*. *Leptoconops mediterraneus* transmits a filarial parasite to donkeys (Foley & Picout-LaForest 1923), and the natural development of *Mansonella ozzardi*, a filarial parasite of humans, has been documented in *L. bequaerti* (Kieffer) (Raccurt & Lowrie 1981).

No studies have addressed the involvement of *Leptoconops* as vectors in the Coachella Valley of southern California, even though several pathogenic agents occur regularly. Arboviruses such as St. Louis encephalitis (SLE), western equine encephalitis (WEE), Hart Park, and Turlock have been isolated annually from culicids (Emmons et al. 1982). In recent years, bluetongue virus (BTV), thus far known to be transmitted only by the ceratopogonid *Culicoides variipennis* (Coq.) (Price & Hardy 1954), has been isolated from bovines (J.C. Turner, University of Wyoming, Laramie, pers. commun.), and high titers of BTV antibodies have been recorded in Desert Bighorn Sheep (Turner & Payson 1982).

Because their potential role in the maintenance of zootic or zoonotic pathogens has not been examined in this region, we initiated studies on the reproductive bionomics of *Leptoconops*, primarily to detect the occurrence of autogeny and whether multiple gonotrophic cycles occur. Six variables of the bionomics of females were examined: spatial and seasonal distribution, host-seeking behavior, rate of insemination, follicular maturation, gonotrophic cycling, and potential longevity and dispersal as measured by prevalence of nectar feeding.

This paper presents data from studies involving *Leptoconops foulki* and *L. knowltoni*, 2 species of the *L. kerteszi* complex that were found to occur during different months near the Salton Sea. A 2nd paper (Brenner & Wargo 1984) describes an outbreak of *L. torrens* Townsend in the Coachella Valley and presents data from our subsequent investigation.

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MATERIALS AND METHODS

Trapping

All studies were conducted within 3 km of the Salton Sea at North Shore in the Coachella Valley, Riverside Co., California (33°32'N, 115°56'24"W, elev. -67 m). Because host-preference profiles of the *Leptoconops kerteszi* complex are not known, we chose to use CO₂ as an activator-attractant unbiased by additional animal emanations. Traps were similar in design to the miniature surveillance trap described by Pfunter (1979) but were modified to eliminate the light and to use 3 alkaline D-cells connected in parallel circuitry. Preliminary tests demonstrated that this trap almost exclusively captured non-blood-fed females with resting stage ovarioles. When placed on the arm these flies immediately engorged. Consequently, we have assumed that flies captured in these traps were seeking a host and thus capture rates hereafter will be termed attack rates.

For several sampling periods, we used paired traps to determine the best height for trapping females. In these instances, traps were positioned 3 m apart and were placed at ground level and at 2 m; the latter was the average maximum height of the predominant vegetation, arrowweed (*Pluchea sericia*). Paired traps were placed at 0, 30, and 100 m from the site of larval development, determined earlier using a brine flotation method to extract *Leptoconops* spp. life stages from soil samples (Brenner & Wargo 1984).

Traps were operated from sunrise to midday (1200 h PST, 1300 h PDT, hereafter designated as AM), at which time collecting bags were changed; trapping then continued from midday until sunset (PM). Females were keyed to species using the criteria of Clastrier & Wirth (1978) involving chaetotaxy of the ultimate antennal segment. The population was monitored twice in March, then once each month through October, with the exception of September. At the beginning and ending of each sampling period, wet- and dry-bulb temperatures, wind speed, and wind direction were recorded.

During the peak abundance of *Leptoconops* in August, 2 additional trapping regimens were followed to further examine distribution and diurnal activity of host-seeking females. Five traps were placed at ground level on a line extending 2.8 km from the larval habitat; traps were operated from 0630–1730 h on 19 August 1981. One trapping period also was devoted to circadian activity; single traps at ground level were placed 0 m, 30 m, and 1.1

km from the larval habitat. These were operated continuously for 24 h; collecting bags were changed every 2 h during the day and night, 1 h before sunset, at sunset, and 1 h after sunset. This procedure of hourly trapping was repeated at the approach of sunrise, with 3 additional 1-h samples beginning 1 h before sunrise (see Fig. 3, sampling period).

Age structure and nectar feeding

From each AM and PM collection, 30–60 females were selected randomly for dissection; equal numbers were taken from each trap. Females were placed in a freezer until they became inactive. The reproductive structures were placed on a glass slide via posterior traction of the last 2 abdominal segments (Linley 1965a). Ovarian tissues were spread with fine needles in a mixture of physiological saline: glycerol (9:1) (Brenner & Cupp 1980) and were examined using phase-contrast microscopy. Parous females were differentiated from nullipars by the presence of follicular relics in the former (Polovodova 1949). For the purpose of this paper, we define "follicular relic" as debris remaining in the tunica following the completion of a gonotrophic cycle. In parous females the state of the follicular relic was categorized either as saccate or dilate (Linley 1965a). Spermathecae were crushed and the presence of spermatozoa noted. Primary follicles were examined and scored for maturation using the criteria of Christophers (1911) and Mer (1936). The remains of dissected midges were placed individually in wells of a porcelain spot plate (Magnarelli 1980) and crushed in 5 drops of cold anthrone reagent (Van Handel 1972). A change in color from yellow to blue within 15 min was interpreted as indicative of recent nectar feeding.

RESULTS

Distribution and activity

Only 2 species of the *Leptoconops kerteszi* complex were captured. *Leptoconops foulki* alone was present during our sampling periods from March through May. This species and *L. knowltoni* were taken in June, and from July through October only *L. knowltoni* was captured. Although the presence of an additional black seta on the last antennal segment is diagnostic for *L. knowltoni*, the color of this seta can be difficult to distinguish. The essentially monotypic collections of March–May and July–October were confirmed by Dr Willis Wirth (USDA-ARS) at the U.S. National Museum in Washington,

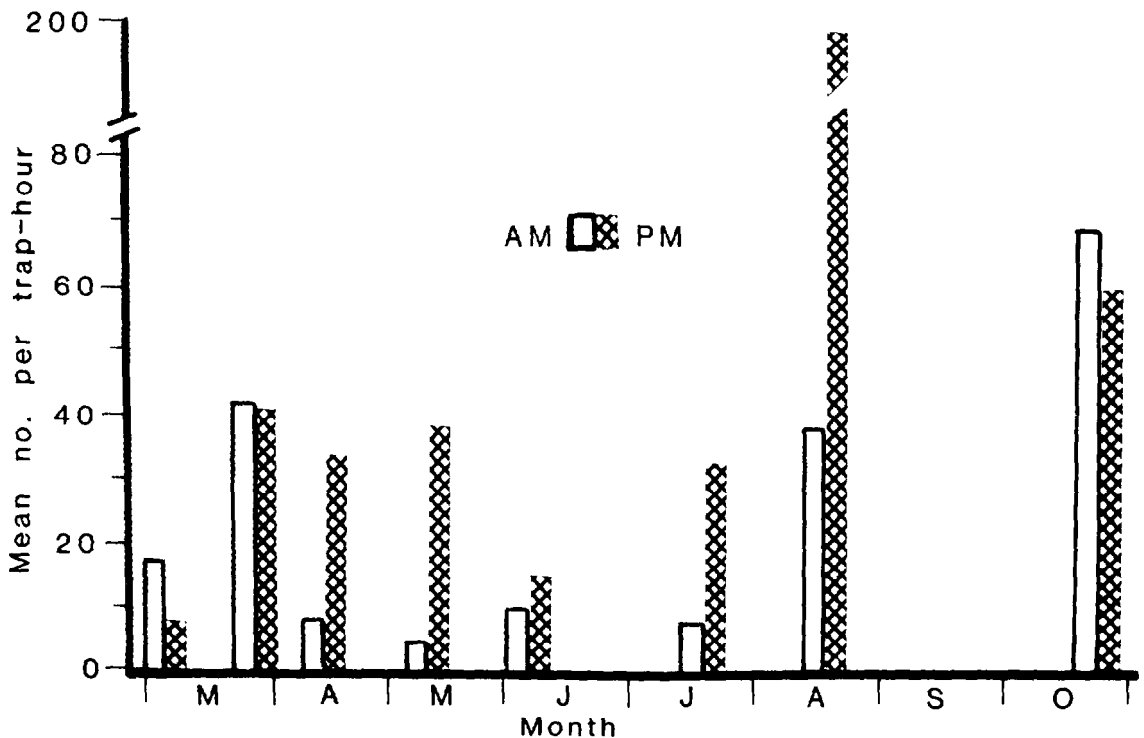


FIG. 1. Mean hourly attack rate of *Leptoconops foulki* and *L. knowltoni* during AM (sunrise to midday) and PM (midday to sunset) of each sample date. Each bar represents data averaged from 30-m and 100-m trap locations (North Shore, Salton Sea, California, 1981). See footnote to Table 3 for species composition.

D.C. Collections in June contained both species. At the time of dissection in the field, specimens could not be identified with certainty. Consequently, data from June cannot be segregated by species.

The mean hourly attack rates of host-seeking *L. foulki* and *L. knowltoni* for each morning and afternoon sample are presented in Fig. 1. These data are quite limited in that the host-seeking population was sampled twice daily on only 8 occasions. Consequently, daily fluctuations owing to changes in weather could not be estimated. However, meteorological conditions in this desert region of southern California varied little throughout the 8-month period: high temperatures recorded during our sampling averaged 34.8 ± 4.9 °C ($\bar{x} \pm SD$, range = 27.2 to 43.3 °C), and winds prevailed from SE-SW at 0.5–6.5 km/h with occasional gusts to 20.8 km/h. Skies were clear or with cirrostratus clouds; no rainfall occurred during the 8 months. Based on our samples, host-seeking populations were minimal in June, the period of transition between species predominance. Population levels of *L. knowltoni* were extraordinarily high in August (198/h), greatly exceeding any level of *L. foulki* that we had encountered.

Attack rates with respect to trap height and location are summarized in Table 1, with statistical analyses in Table 2. Regardless of location, traps at ground level captured more host-seeking females than did traps at the 2-m level. Furthermore, at the lower trap height, attack rates were significantly greater at 30- and 100-m locations compared to the location within the larval habitat (0 m); differences between 30- and 100-m locations were not significant. Differences at the higher trap position were not significant among any trap locations.

The effect of distance from the larval habitat on attack rates of *L. knowltoni* is presented in Fig. 2. Although attack rates dropped by nearly 50% within the first 0.5 km, host-seeking females were captured at the maximum trapping distance of 2.8 km. This farthest trap was 100 m from an open fresh-water irrigation canal. The higher attack rate at this location, as compared to the rate at 1.95 km, was confirmed in a 2nd period of trapping (data not presented). The canal, with its treeless, steep, clay-lined banks, cannot support larval *Leptoconops*. However, it may serve either as a source of water or as a physical barrier, with a resultant increase

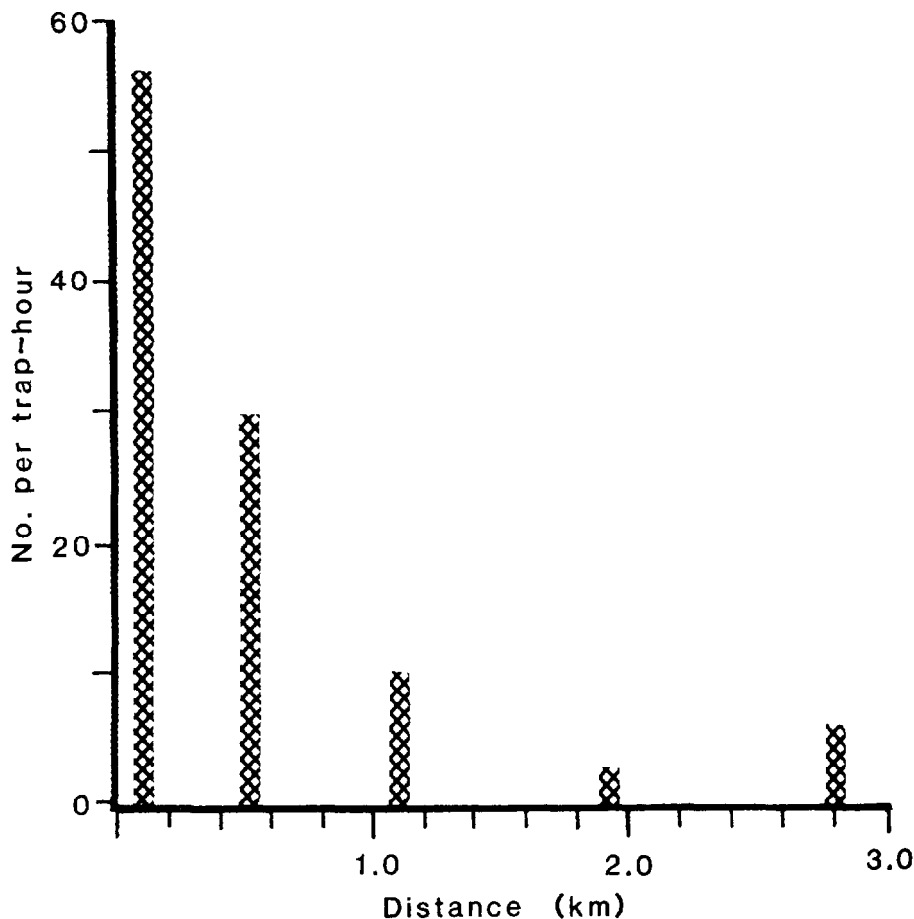


FIG. 2. Effect of distance from the larval habitat on the attack rate of *Leptoconops knowltoni* as measured by the number of host-seeking ♀ captured per hour from 0630–1730 h in CO₂-baited traps (North Shore, Salton Sea, California, 19 August 1981).

in density of adults near its banks. Data transformed to log catch (Y) vs. distance (X) (2.8 km location ignored) fit the equation $\log Y = 1.83 - 0.698X$ ($r^2 = 0.999$, plot not presented).

Leptoconops knowltoni exhibited a bimodal diurnal distribution (Fig. 3). The 1st peak occurred within

the 1st hour of daylight when winds were calm and humidity high. Following a period of lesser activity (0800–1330 h) during which wind had increased to 2–12 km/h, host-seeking activity increased sharply (1330–1730 h) while wind remained strong at 6–12 km/h; humidity was low during the afternoon peak. Activity ceased shortly after sunset.

TABLE 1. Attack rates [mean number per hour (range)] of *Leptoconops foulki* and *L. knowltoni* in ground-level and 2-m level CO₂-baited traps at 3 distances from the larval habitat at North Shore on the Salton Sea, California, March–October 1981.

TRAP HEIGHT (m)	DISTANCE FROM LARVAL HABITAT (m)		
	0	30	100
0	17.2 (0–87.4)	56.8 (4.9–183)	68.3 (11.1–213.5)
2	1.0 (0–2.4)	9.1 (0.1–23.2)	9.7 (0.9–20.4)

Nectar imbibition

Our study on nectar imbibition was designed to serve as an indicator of potential to disperse and survive (longevity). A summary of our findings on 572 host-seeking females is presented in Table 3. Of these, 68% were anthrone-positive, indicating recent nectar imbibition. Chi-square analysis indicated that the proportion of nectar-fed females was dependent on the date sampled ($\chi^2 = 21.13$, 7 df, $P < 0.005$). However, cell values for the 1st sample contributed 12.33 to the chi-square total;

TABLE 2. Statistical comparisons of capture rates of host-seeking *Leptoconops foulki* and *L. knowltoni* at paired ground-level (L) and 2-m level (H) CO₂-baited traps at 3 distances from the larval habitat at North Shore, Salton Sea, California, March–October 1981.

STATISTICAL COMPARISON*	t	df	P
L vs. H			
0 m	3.48	9	<0.01
30 m	4.91	7	<0.003
100 m	7.00	7	<0.001
0 m vs. 30 m			
L	5.22	12	<0.001
H	2.13	7	=0.07
30 m vs. 100 m			
L	0.98	12	NS
H	0.24	7	NS
0 m vs. 100 m			
L	6.80	12	<0.001
H	1.53	7	NS

* Based on paired *t*-tests applied to data transformed to $\log(n+1)$ where *n* = number captured/hour (Snedecor & Cochran 1967).

a variance test for homogeneity (Snedecor & Cochran 1967), using data from the last 7 sampling dates, confirmed homogeneity of proportions ($\chi^2 = 8.258$, 6 df, $P = 0.23$). Additional analyses indicated that the proportion of the population that was anthrone-positive was independent of time of day sampled ($\chi^2 = 0.0027$, 1 df, corrected for continuity, $P > 0.9$) and of distance from the larval habitat ($\chi^2 = 0.747$, 1 df, corrected for continuity, $P > 0.3$).

Gonotrophic age

Gonotrophic age-grading of 598 host-seeking females captured at all 3 locations revealed that a substantial proportion (>15%) of the population was parous on all sampling dates (Table 4). The proportions of parous females in the *L. foulki* populations in March and April were not significantly

different ($\chi^2 = 0.067$, 2 df, $P > 0.95$). By May, however, a significant aging of the population had occurred; nearly 90% were parous. The population in June was presumed to reflect a state of transition between *L. foulki* females (senescent) and *L. knowltoni* females (emergent); hence, the parous rate was moderate (54%). The *L. knowltoni* population was sampled 3 times from July through October. Percentages of parous females varied from 38 to 58; differences were not significant ($\chi^2 = 5.656$, 2 df, $P = 0.062$). Excluding the period of senescence of *L. foulki* populations (12.V) and the period of transition between species (2.VI), differences between parous rates of *L. foulki* and *L. knowltoni* were significant (ANOVA, arcsin transformation of proportions, $F_{1,4} = 24.37$, $P < 0.025$; Snedecor & Cochran 1967).

In July, August, and October, 28 bipars of *L. knowltoni* were discerned; 15 were captured at the 0-m location. Most ovarioles in biparous females exhibited a compact dilatation, containing highly refractile particles, positioned below (toward the calyx) a typical saccate-type relic; a constriction in the tunica separated the 2 relics. The ultimate follicles in biparous females commonly were in stages N or I. In 3 additional instances, evidence of a triparous condition was seen. However, it was difficult to resolve 2 compact dilatations with confidence.

Gonotrophic aging was analyzed further by segregating data on the basis of the time of day host-seeking females were captured (Table 5). Morning and afternoon populations differed significantly in the proportion parous; parous females were encountered more commonly in the afternoon ($P < 0.005$). This biting cycle was most pronounced in March, April, August, and October (Fig. 4). In May, June, and July the differences in age structure were negated by the senescence of the populations. Parous rates were independent of trap location (Table 5, $P = 0.057$).

Additional evidence of cyclical behavior in these

TABLE 3. Summary of results of the anthrone test used to detect nectar in the crop of host-seeking *Leptoconops foulki* and *L. knowltoni* captured in CO₂-baited traps at North Shore, Salton Sea, California, 1981.*

	DATE SAMPLED								TOTAL
	10.III	19.III	14.IV	12.V	02.VI	14.VII	19.VIII	27.X	
No. tested	37	84	114	64	80	51	95	47	572
Proportion +	0.4054	0.6310	0.7368	0.7188	0.7250	0.7451	0.7053	0.5532	0.6766

* Species composition: 10.III–12.V, *L. foulki*; 02.VI, *L. foulki* and *L. knowltoni*; 14.VII–27.X, *L. knowltoni*.

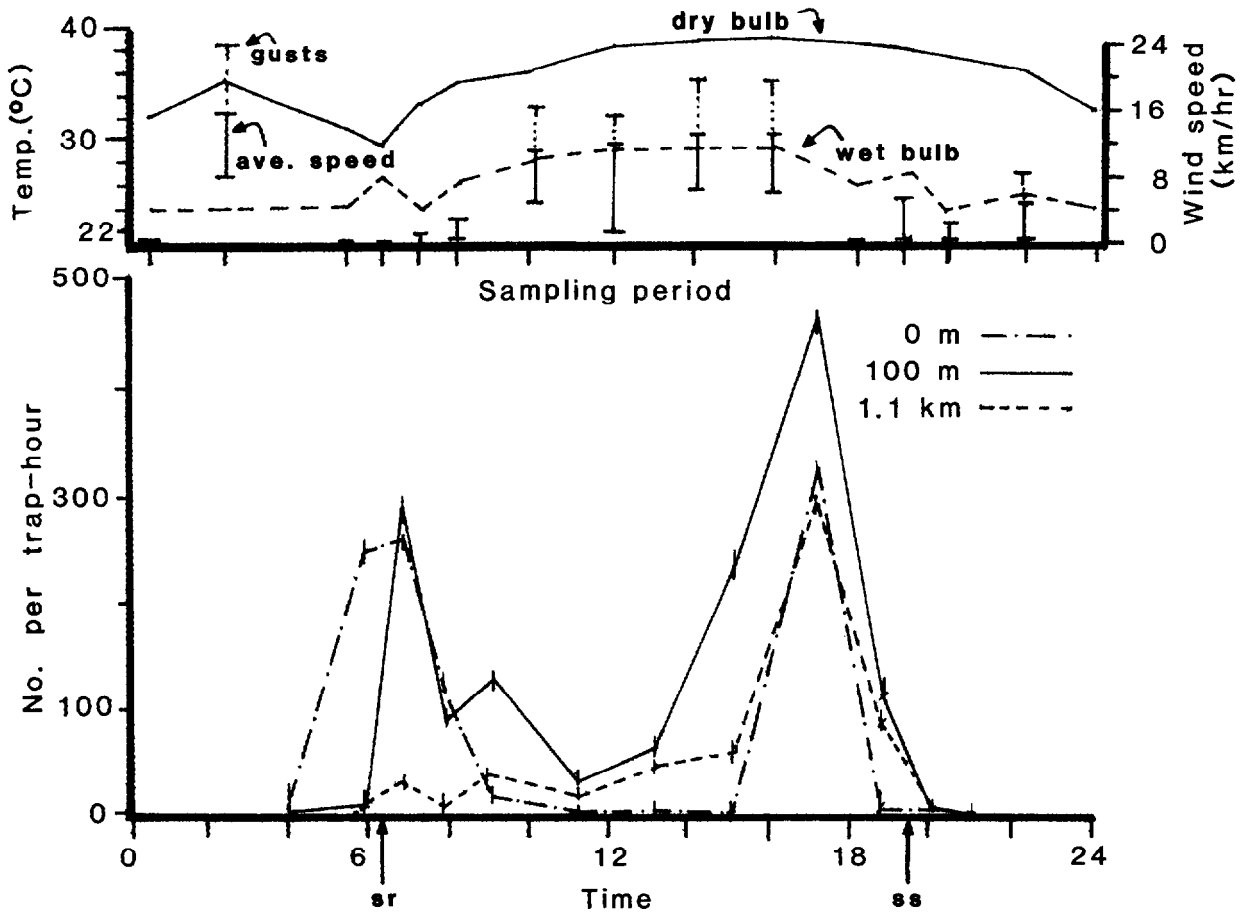


FIG. 3. The circadian activity of host-seeking *Leptoconops knowltoni* at 0 m, 100 m, and 1.1 km from the larval habitat near the Salton Sea, California, and associated meteorological data (24–25 August 1981). sr = sunrise, ss = sunset.

populations of *Leptoconops* was seen in the distribution of follicular relics; saccate and early dilate relics are illustrated in Fig. 5a and b, respectively. Table 6 contains a summary of 233 observations on follicular relics pooled by time sampled and location. Females with saccate follicular relics, indicative of recent oviposition, were captured more

commonly in the afternoon ($P < 0.005$); when pooled by location, no significant difference was noted ($P = 0.23$).

Follicular maturation and insemination

Follicular maturation in host-seeking females was arrested in stage I–II, with a well-defined oocyte,

TABLE 4. Summary of parity and gonotrophic age-grading of *Leptoconops foulki* and *L. knowltoni* by date sampled at North Shore, Salton Sea, California, 1981.* See text for statistical treatment.

	DATE SAMPLED								TOTAL
	10.III	19.III	14.IV	12.V	02.VI	14.VII	19.VIII	27.X	
No. dissected	38	85	114	66	83	60	102	50	598
No. uniparous	6	17	25	58	45	23	40	16	230
No. biparous	0	0	0	0	0	4	18	2	24
No. triparous**	0	0	0	0	0	1	1	1	3
Proportion parous	0.1579	0.2000	0.2193	0.8788	0.5422	0.4667	0.5784	0.3800	0.4298

* Species composition: 10.III–12.V, *L. foulki*; 02.VI, *L. foulki* and *L. knowltoni*; 14.VII–27.X, *L. knowltoni*.

** See text.

TABLE 5. Analyses of parity of *Leptoconops foulki* and *L. knowltoni* pooled by time of day or location. North Shore, Salton Sea, California, March–October 1981.

POOLED BY		NO. DISSECTED	NO. NULLIPAROUS	NO. PAROUS	PROPORTION PAROUS	SIGNIFICANCE
Time	AM	295	202	93	0.3153	$\chi^2 = 30.272$ $P < 0.005$
	PM	303	139	164	0.5413	
	Total	598	341	257	0.4298	
Location	0 m	120	58	62	0.5167	$\chi^2 = 5.776$ $P = 0.057$
	30 m	240	148	92	0.3833	
	100 m	238	135	103	0.4328	
	Total	598	341	257	0.4298	

TABLE 6. Analyses of state of follicular relics in parous *Leptoconops foulki* and *L. knowltoni* pooled by time of day or location. North Shore, Salton Sea, California, March–October 1981.

POOLED BY		NO. DISSECTED	NO. SACCATE	NO. DILATE	PROPORTION SACCATE	SIGNIFICANCE
Time	AM	90	27	63	0.3000	$\chi^2 = 19.87$ $P < 0.005$
	PM	143	87	56	0.6084	
	Total	233	114	119	0.4893	
Location	0 m	62	36	26	0.5806	$\chi^2 = 3.042$ $P = 0.23$
	30 m	78	37	41	0.4744	
	100 m	93	41	52	0.4409	
	Total	233	114	119	0.4893	

TABLE 7. Stage of follicular development and success in mating of host-seeking ♀ of *Leptoconops foulki* and *L. knowltoni*. North Shore, Salton Sea, California, 1981.

NO. DISSECTED	NO. MATED (%)	NO. PER STAGE OF FOLLICULAR DEVELOPMENT (%)						
		N	I	I–II	II	III	IV	V
598	582 (97.8)	34 (5.7)	87 (14.5)	473 (79.2)	2* (0.33)	1* (0.17)	1* (0.17)	0

* Partial blood meal evident in gut.

7 nurse cells, and a few yolk droplets (Fig. 6, Table 7); 97.8% were mated. Approximately 20% had not achieved the resting stage when dissected, and most of these were parous (59%). Only 4 females exhibited follicles beyond stage I–II, and in each case a partial blood meal was evident in the gut. Hence, we consider these species to be anautogenous (Clements 1963).

On rare occasions we found partially or wholly engorged females in our traps. Consequently, we undertook a simple investigation to determine if females fed once to repletion could complete an ovarian cycle. Wild-caught females of *L. foulki* were permitted to feed to repletion on the forearm; others were offered 10% sucrose only. All were maintained on 10% sucrose and distilled water at 26 °C except for hours 24–36 when females were held at 22 °C. Four to 6 females were dissected at in-

tervals to monitor development of ova. Sugar-fed females were dissected occasionally and verified that follicular maturation was arrested at stage I–II.

Females exhibited gonotrophic concordance (Table 8); 1 blood meal was sufficient for development from the resting stage to full maturation (stage V) in 84 h or less at 26 °C. One female had oviposited by 84 h but had retained 2 eggs. Egg retention also was seen in 22 of 341 parous females (6.5%) dissected during our routine studies at North Shore. Such females rarely retained more than 1 or 2 eggs.

Nuisance index and vector potential

A nuisance index is presented in Fig. 7a. Derived by multiplying the attack rate by the proportion nulliparous, this index reflects the number of nul-

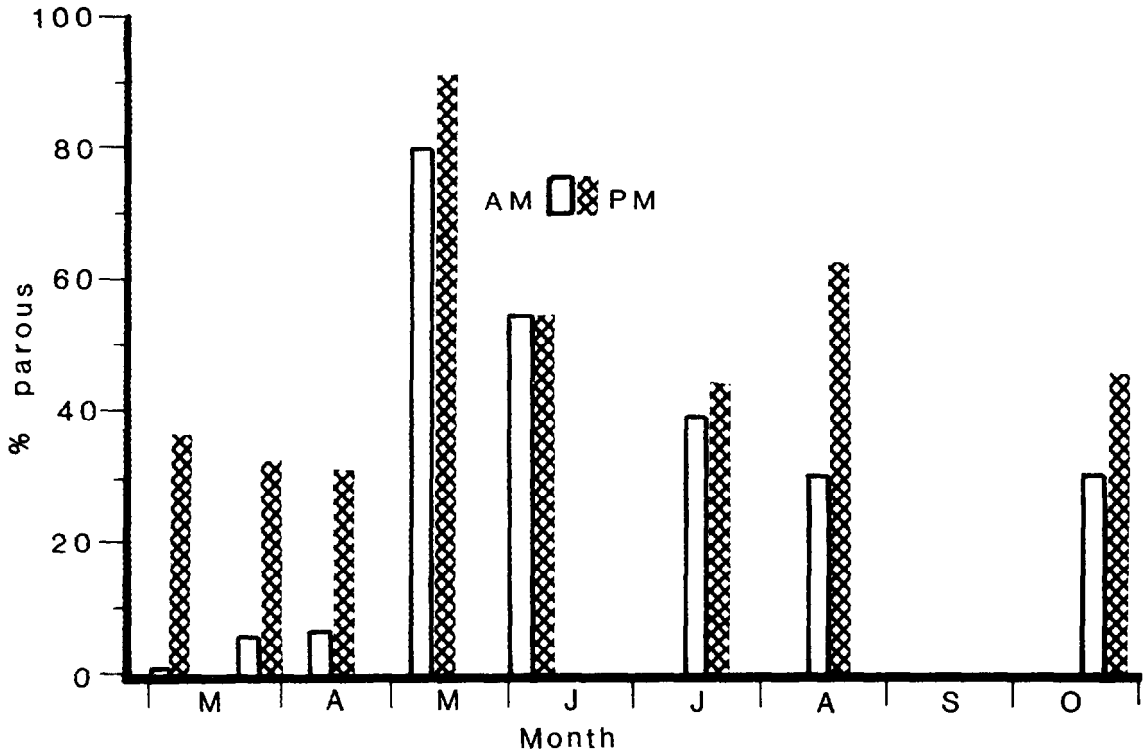


FIG. 4. Parity of *Leptoconops foulki* and *L. knowltoni* by AM (sunrise to midday) and PM (midday to sunset) of each sample date. Each date represents data averaged from 30-m and 100-m trap locations (North Shore, Salton Sea, California, 1981). See footnote to Table 3 for species composition.

liparous females seeking a blood meal per hour. If *Leptoconops* midges are involved in the cycling of pathogens, and if transovarial transmission does not occur, the bites of nulliparous females are principally a nuisance. Differences in the magnitude of AM and PM peaks do not follow a uniform pattern. In contrast, the biting cycle described earlier is apparent when the mean attack rate of parous midges is plotted by time and date sampled (Fig. 7b). Data presented in this manner provide an index of vector potential (Crans et al. 1970). Three points can be clearly interpreted. The risk of encountering parous host-seeking females is always greater in the afternoon. Parous females were captured in greatest numbers in May and August. Finally, vector potential in July, August, and October (and presumably in September) is enhanced by the presence of multipars.

DISCUSSION

Our data on seasonal distribution indicate that *L. foulki* is abundant at the Salton Sea from March through May, is reduced in numbers in June, and is replaced by *L. knowltoni* from July through at

least October. Foulk (1969) studied the activity of a species referred to as *L. kerteszi* at the Salton Sea, but only in March and April. When the *L. kerteszi* complex was revised into 12 species, Clastrier & Wirth (1978) referred to the species as *L. knowltoni*, apparently because the holotype and allotype of this species were collected by Foulk at North Shore. This apparent contradiction in our work vs. Foulk's may be resolved by the distribution records of Clastrier & Wirth; type-specimens of *L. knowltoni* were collected in September, not during the time encompassed by Foulk's study. Hence, Foulk's article was erroneously listed under the synonymy of *L. knowltoni* instead of *L. foulki* (W.W. Wirth, U.S. National Museum, pers. commun.)

Even though routine trapping did not extend beyond 100 m from the larval habitat, our data indicate that appetential movement away from this site is common. *Leptoconops foulki* and *L. knowltoni* females are adept at procuring carbohydrates and might be expected to engage in extensive host-seeking as has been reported commonly in Diptera (Downes 1958, Clements 1963, Hocking 1968). Observations on the seasonal and circadian activity

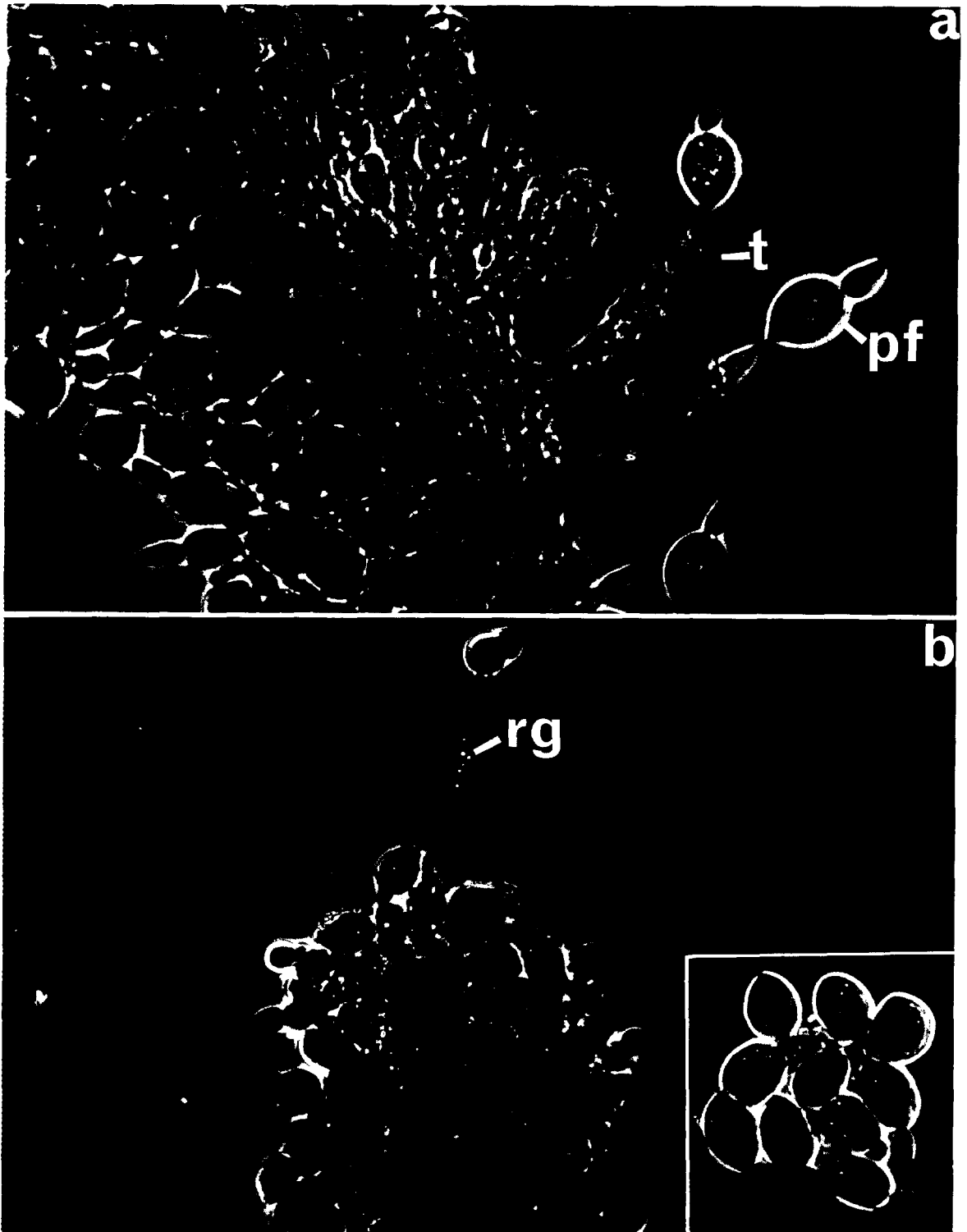


FIG. 5. Typical saccate (a) and early dilate (b) follicular relics in ovarioles of parous *Leptoconops kerteszi* complex ♀♀ captured at North Shore, Salton Sea, California, October 1981. pf = primary follicle, rg = refractile granules, t = tunica of relic. Inset, follicles from a nulliparous ♀.



FIG. 6. The resting stage (I-II) of a primary follicle in a typical nulliparous *L. kerteszi* complex ♀ captured at North Shore, Salton Sea, California, October 1981. nc = nurse cell, on = oocyte nucleus, y = yolk.

of the *L. kerteszi* complex, and on the effect of distance from the larval habitat on attack rates, confirm that these species are a nuisance in the Salton Sea basin for much of the year.

Attack rates show that host-seeking females are captured more effectively by traps at ground level. Although this suggests that females remain close to the ground when seeking a host, the micro-movements of the CO₂ during each trapping period were not known; consequently, definitive conclusions regarding the stratification of host-seeking midges cannot be drawn.

There is some indication that the attack rate at North Shore tends to be greater in the afternoon (paired *t*-test, *P* = 0.08). Foulk (1969) reported bimodal activity of *L. foulki* at the Salton Sea, but his data show no evidence that the magnitudes of peaks differed. However, 2 points must be considered. Our samples taken during the comparable period (March) also failed to show significant differences in attack rates. Secondly, in Foulk's studies, adults were captured by a D-VAC aspirator carried by the collector as he walked throughout the larval habitat. Adults captured in this manner may have been disturbed from their resting sites by the

movement of the collector and may not have been seeking a host. Lacking data on the physiological state of these midges, interpretation of these populations as host-seeking females is not valid. In our

TABLE 8. Follicular maturation in blood-fed, wild-caught *Leptoconops foulki*. Adults were maintained at 25.6 °C except for hours 24-36 when they were held at 21.6 °C. North Shore, Salton Sea, California, 1981.

HOUR POST-ENGORGEMENT	NO. PER STAGE OF ULTIMATE FOLLICLE*					
	I-IIA	I-IIB	II	III	IV	V
18	2**		3			
24	1**†	1	2	1		
38		1***	2	2		
48			2	3		
60		1†	1	2	1	
84						4††

* Stage I-II has been divided to distinguish a resting follicle (I-IIA) from a developing follicle (I-IIB) that has not yet reached stage II.

** One was parous and therefore entering its 2nd gonotrophic cycle.

*** Partial blood meal.

† Mite attached.

†† One had deposited 100 eggs and retained 2.

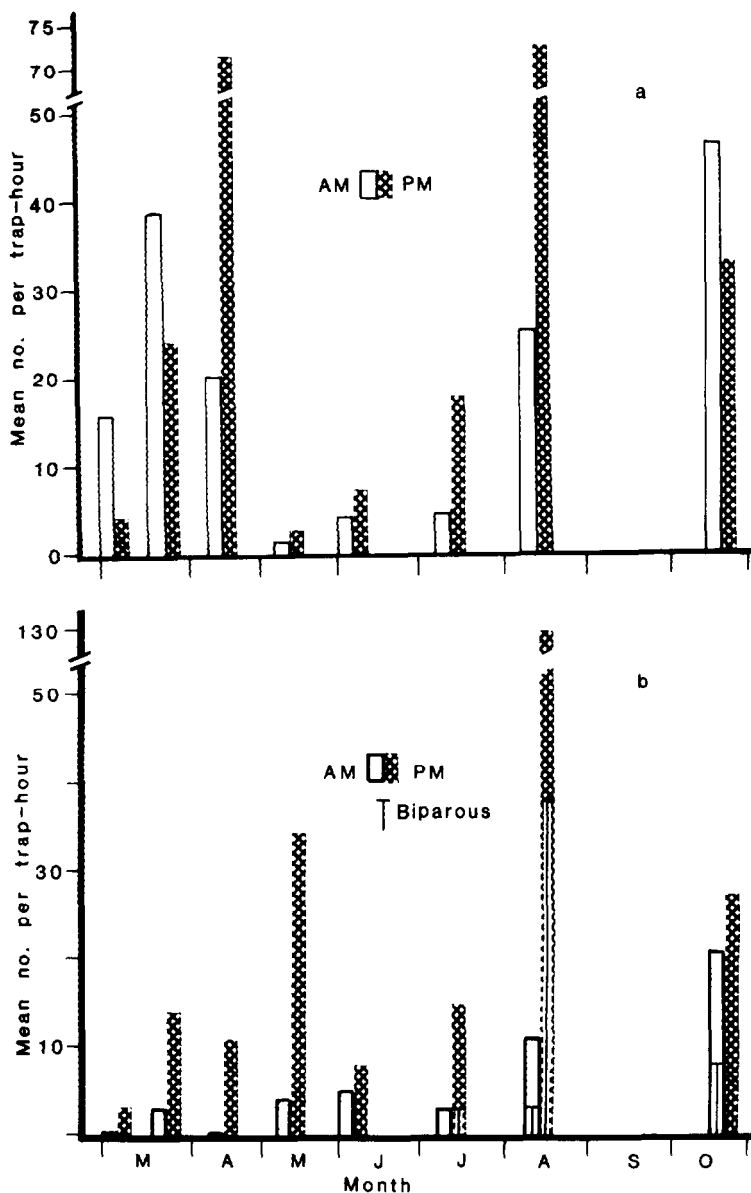


FIG. 7. Mean attack rates of nulliparous (a) and parous (b) midges of *Leptoconops foulki* and *L. knowltoni* during AM (sunrise to midday) and PM (midday to sunset) of each sample date. Each bar represents data averaged from 30-m and 100-m trap locations (North Shore, Salton Sea, California, 1981). See footnote to Table 3 for species composition.

studies catches contained, almost exclusively, mated females with follicles at the resting stage and without blood in the gut. We conclude that these midges were physiologically competent to ingest blood and actively sought the source of CO_2 ; hence, they were seeking a host.

The reduced catches during the morning activity peak may have been partly the result of a characteristic lack of wind soon after sunrise (exemplified in Fig. 3). We have noted during the course of these investigations, and in others (Brenner et al. 1984),

that the largest catches occur when winds are 8–16 km/h. In the absence of wind, CO_2 probably is dispersed poorly and consequently fewer females are captured. Kettle & Linley (1967) examined the effects of meteorological conditions on the biting activity of *L. bequaerti* in Jamaica and demonstrated that winds greater than 24 km/h halted biting activity, that speeds above 8 km/h had an inhibitory effect, and that biting rates increased as wind speed increased to 8 km/h; the last observation also may have been related to decreasing light levels.

However, in addition to the influence of wind, our data indicate that the relative intensity of morning and afternoon attack rates may be related to the gonotrophic age of the population at large. For example, winds were light (<8 km/h) and relatively steady from the SSE during sampling periods in late March and May; consequently, we can assume with reasonable confidence that differences in attack rates in AM vs. PM periods were affected minimally by wind. Sampling in late March indicated a slightly higher attack rate for *L. foulki* in the morning (Fig. 1). This population was almost exclusively nulliparous (Fig. 4) and was near our measured seasonal peak, with an average daily parous rate of 20% (Table 4). In contrast, the lowest morning attack rate for *L. foulki* occurred in May when the population appeared to be diminishing; the average daily parous rate was 88%. This suggests that when a female converts from a nulliparous to a parous state, she will be more inclined to seek a host in the afternoon than in the morning. This trend, referred to as a biting cycle, is documented in our study and supports the concept that a bimodal pattern of activity in a host-seeking population is not primarily the result of a consistent character in an individual, but rather is the result of a change in character as an individual becomes senescent. This concept was postulated by Kettle & Linley (1967) when they stated, "Where there are 2 periods of activity, it is likely that any particular individual will only be involved in one"

This biting cycle may be due primarily to the timing and synchrony of oviposition. Our data on the state of follicular relics suggest some synchrony of oviposition; parous females with saccate follicular relics predominate in the afternoon (Table 6). Linley (1965a) found that saccate relics uniformly contracted to the dilate state in 16 h in *L. bequaerti*. If this rate is assumed to hold for the *L. hertesi* complex, oviposition likely occurs in the morning. Our data indicate that nulliparous females are as likely to seek a host in the morning as they are in the afternoon, but host seeking by parous females is relatively synchronous, occurring primarily in the afternoon. If most females deposit eggs at the same time of day, it is plausible that parous females would begin to seek a host in unison.

Based on the pattern of follicular maturation in host-seeking females, both species at the Salton Sea are anautogenous. We confirmed this in *L. foulki* and demonstrated gonotrophic concordance. This

can be presumed also for *L. knowltoni*, although similar laboratory studies were not undertaken. It could be argued that high parous rates might be indicative of autogeny in at least a portion of the *L. knowltoni* population. Schmidtman & Washino (1982) discovered autogeny in *L. carteri* in north-central California and found parous rates near 100%; the few nulliparous females exhibited follicular development beyond the resting stage. In our studies, follicles in non-blood-fed females were never beyond the resting stage. Hence, it is unlikely that autogeny occurs in the *L. knowltoni* population at any significant level.

It might also be argued that the high parity rates were false because relics were the result of oosorption. Mullens & Schmidtman (1982) found that this occurred commonly in *Culicoides variipennis* in laboratory studies but concluded that it is probably rare in field populations. If oosorption occurs as a result of partial blood meals, the impact on vector potential is largely the same; anautogenous females with relics are seeking their 2nd blood meal and consequently may be capable of mechanical or biological transmission of pathogens.

Vector potential is also related to the longevity of the anautogenous female and the length of the gonotrophic cycle. In *L. foulki*, we have determined that females need ca. 84 h at 25.6 °C to mature eggs after a blood meal. Linley (1965b) found that follicular maturation in *L. bequaerti* ranged from 27 h at 36.6 °C to 98 h at 20 °C. In the Salton Sea basin, desert nights from March to May can be quite cool (5–15 °C), with means well below 25 °C; consequently, follicular maturation may require substantially more than 84 h. In contrast, desert nights from June through mid-September are warm, and low temperatures commonly are greater than 25 °C; daytime highs may average 40–45 °C. Therefore, follicular maturation in *L. knowltoni* may be rapid, resulting in high parous rates from July through October. Hence, the occurrence of multiparous females during that period might be due primarily to this temperature-related phenomenon rather than to a longer life-span compared to *L. foulki*.

Acknowledgments. We wish to acknowledge the Coachella Valley Mosquito Abatement District and its Manager, Cpt. G.S. Stains, for support of the project and for the use of their facilities. We also acknowledge Dr W.W. Wirth, U.S. National Museum, for verifying and/or identifying specimens of *Leptocnops*, and Drs J.R. Linley and E.W. Cupp for their criticisms of an earlier draft.

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