Bionomics of *Anopheles quadrimaculatus* and *Culex erraticus* (Diptera: Culicidae) in the Falls Lake Basin, North Carolina: Seasonal Changes in Abundance and Gonotrophic Status, and Host-Feeding Patterns

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ABSTRACT Larval and adult *Anopheles quadrimaculatus* Say (sensu lato) and *Culex erraticus* (Dyar & Knab) were collected at Falls of the Neuse Lake (Falls Lake) in North Carolina from May 1985 to December 1986. Adult mosquitoes were aspirated weekly from shelters in woodlands adjacent to larval sampling sites. *An. quadrimaculatus* and *Cx. erraticus* comprised >95% of the total number of mosquitoes collected. *An. quadrimaculatus* adults exhibited vernal and autumnal peaks of abundance during both years. *Cx. erraticus* adults exhibited several peaks of abundance in summer and early fall of both years. *An. quadrimaculatus* initiated blood feeding in May and April 1985 and 1986, respectively. Only unfed females were found in late fall and winter. *Cx. erraticus* initiated blood feeding earlier than *An. quadrimaculatus*. In 1985, ≈25% of the females in the first collection in May contained a blood meal, whereas in 1986, ≈10% of the females in the first collection in April were blood fed. Females of both species ceased blood feeding in late fall. Larvae were sampled on a weekly basis from lake edge, flood plain, and creek edge habitats. Generally, *An. quadrimaculatus* larvae were most abundant in lake edge and flood plain habitats, whereas *Cx. erraticus* larvae were most abundant in the creek edge habitat. The population dynamics of *An. quadrimaculatus* were associated with seasonal changes in the level of Falls Lake. In 1985 and 1986, the level of Falls Lake gradually declined from May to mid-August until heavy rainfall caused a 1-m rise in lake level. Populations of *An. quadrimaculatus* larvae and adults increased significantly following the rise in the level of Falls Lake. In contrast, the abundance of larval and adult *Cx. erraticus* decreased with rising lake levels in late August. Water level management should be an effective method for controlling populations of *An. quadrimaculatus* but not for *Cx. erraticus*. Blood-fed mosquitoes were tested to identify bloodmeal hosts using both capillary precipitin and enzyme-linked immunosorbent assays. *An. quadrimaculatus* (n = 941) predominantly (99%) fed on mammals, principally white-tailed deer and horses. *Cx. erraticus* (n = 348) exhibited an opportunistic host-feeding pattern; blood meals were taken from mammalian (49%), reptile or amphibian (20%), and avian (31%) hosts.

KEY WORDS *Anopheles quadrimaculatus, Culex erraticus,* bionomics

THE IMPOUNDMENT OF RIVERS often creates breeding habitats for mosquitoes along lake edges and flood plains of reservoirs (Carter 1915, Barber et al. 1924, Gage 1925, TVA 1947, Hess & Crowell 1949). *Anopheles quadrimaculatus* Say (sensu lato) and *Culex erraticus* (Dyar & Knab) are the most abundant pest mosquitoes found breeding in TVA impoundments (Gartrell et al. 1981). Historically, malaria epidemics were associated with impoundments constructed in areas where the disease was endemic. Control programs in years subsequent to these epidemics were directed at reducing the production of anopheline mosquitoes. Responsibility for vector control generally was accepted by government agencies such as the TVA and the U.S. Army Corps of Engineers for their impoundments. Although malaria has been eliminated, these agencies still administer programs in which anopheline mosquito populations are monitored and managed. In the early 1980s, the U.S. Army Corps of Engineers constructed Falls Lake Reservoir, a 4,800-ha impoundment in the northeastern Piedmont region of North Carolina. In 1985 and 1986, mosquito populations pro-

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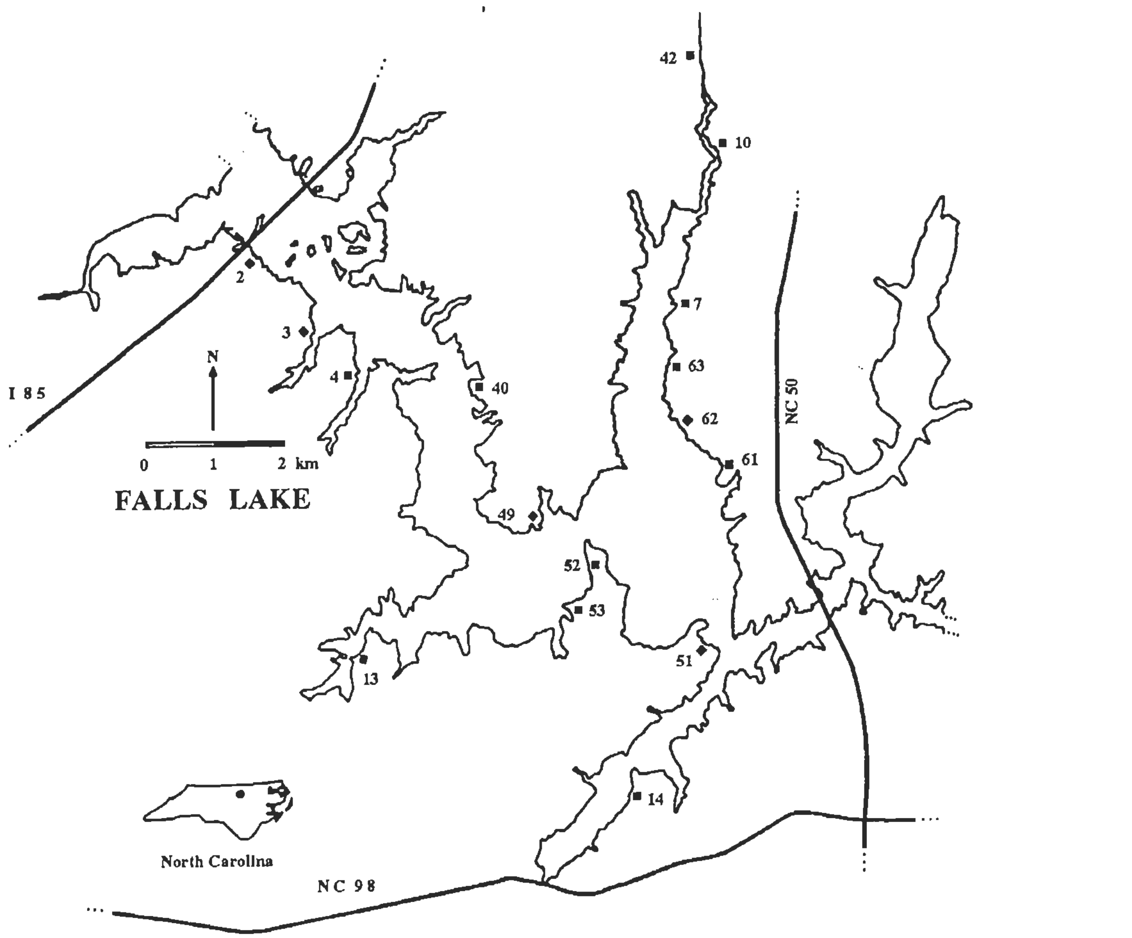

Fig. 1. Map of Falls Lake basin showing the locations of resting shelters and larval sampling sites.

duced in and adjacent to Falls Lake were routinely sampled.

The biology of *An. quadrimaculatus* in the Southeast is well studied (Boyd 1927, Balfour 1928, Boyd & Weathersbee 1929, TVA 1947, Hitchcock 1968) because of its involvement in transmission of malaria, but comparable studies are lacking for *Cx. erraticus*. Our report presents results of field studies on the bionomics of mosquito species that are relevant to development of a management plan for mosquito populations in the Falls Lake basin. The specific objectives of our research were to determine effects of seasonal changes in the level of Falls Lake on the population dynamics of *An. quadrimaculatus* and *Cx. erraticus*, and to characterize the blood-feeding activities of these mosquitoes in the Falls Lake basin.

Materials and Methods

Area of Investigation. Field work was conducted from May 1985 to December 1986 in Falls Lake basin in an area located in Wake, Durham, and Granville counties, NC (Fig. 1). The study area, bounded by highways I-85, N. N. 98, and N. C. 50, was chosen on the basis of its proximity to present and future public use areas, human habitation, and the potential for prolific mosquito production. This portion of the reservoir was characterized by a gradually sloping shoreline with emergent vegetation. With seasonally changing lake elevations, lowland areas periodically were flooded, especially after heavy rainfall. Vegetation surrounding the lake consisted mostly of early, middle, and climax oak–hickory successional communities as well as old fields, pure pine, and oak–hickory–pine forests.

Sampling and Handling Adult Mosquitoes. Mosquitoes were collected from resting shelters located in shaded woodlands adjacent to the lake (Fig. 1). The rectangular-shaped shelters (2.1 m high, 1 m wide, 1 m deep) were constructed of plywood with the exteriors painted dark green and the insides left unpainted. Dark-colored cloth material was placed across the top 50 cm of the open front of each shelter to darken the interior. Shelters in upland areas were positioned in stands of trees with the open side facing west to assure that they were shaded in late mornings and early afternoons (Morris 1981). Shelters located near a swamp edge were positioned to face the swamp. The shelters were placed within 50 m of the lake with one exception: site 42, which was located adjacent to a creek that flowed into the reservoir. Collections of mosquitoes were made weekly from April through November and monthly during December through March. Mosquitoes were collected between 1000 to 1400 hours EDT from 14 shelters in 1985 and 16 shelters in 1986.

Mosquitoes were collected using a hand-held mechanical aspirator, placed immediately in a cooler on dry ice, transported to laboratory facilities, and processed immediately or temporarily stored at −20°C. A chill table was used during the sorting and identification of mosquitoes to keep specimens frozen. Mosquitoes in each collection were identified to species and sex, and counted. Voucher specimens of each mosquito species collected were deposited in the Insect Collection in the Department of Entomology at North Carolina State University. Females of *An. quadrimaculatus* and *Cx. erraticus* were externally examined, dissected if necessary, and classified as either empty, blood fed, or gravid. Blood-fed mosquitoes were stored at −80°C until used for host determination.

Sampling and Handling Mosquito Larvae. The aquatic habitat adjacent to each resting shelter was sampled for mosquito larvae on a weekly basis with a standard 473-ml (1 pint) dipper. At each site, a one-dip collection was taken for every ≈0.5 m^2 of habitat that would likely harbor mosquitoes. All larvae and pupae collected were concentrated into a single sample which was immediately preserved with ethyl alcohol. Larval surveys were conducted in lake edge, flood plain, and creek edge habitats. The lake edge habitat was characterized by shallow, vegetated edges of Falls Lake that were in the open or contained standing timber. Harborage for mosquito larvae was provided by woody debris, black willow, *Salix nigra,* stems, smartweed, *Polygonium* sp., and annual grasses. The lake edge was sampled weekly at 14 sites in 1985 and 16 sites in 1986. Flood plain habitats consisted of expanses of open shallow water containing clumps of *Juncus* spp., black willow stems, annual grasses, and large expanses of *Aster* sp. Flood plain areas varied markedly in size with changes in lake level. Only small (<0.5 m) changes in lake elevation were necessary to inundate or expose these shallow, flat areas. One flood plain site was sampled weekly because only one shelter was located next to a flood plain. Creek edge habitats consisted of isolated pools in creek beds or along the margins of creeks with little or no water flow. This habitat was largely devoid of vegetation. Mosquitoes were concentrated around snags and floating woody debris. Four major creeks entered Falls Lake in the study area. Weekly sampling of creek edge consisted of one site because only one resting shelter was located adjacent to a creek.

In the laboratory, mosquito larvae and pupae were identified and an average per dip for *An. quadrimaculatus* and *Cx. erraticus* was calculated for that week. This average was obtained by dividing the total number of larvae of a species collected in all habitats combined or in each habitat by the total number of dips taken in all habitats or for each specific habitat, respectively.

Identification of Hosts of Blood-Fed Mosquitoes. Hosts were identified with the capillary precipitin technique (CPT) and enzyme-linked immunosorbent assay (ELISA) as previously described (Irby & Apperson 1988). Blood-fed mosquitoes were ground and extracted in a phosphate buffer saline solution, and the CPT was used with undiluted general screening antisera to determine if the blood meals were of mammalian, amphibian–reptilian, or avian origin. Those blood meals that reacted were further screened to determine the specific hosts using the CPT for avian blood meals or the ELISA for mammalian, amphibian, and reptilian blood meals.

Rainfall and Lake Elevation. Measurements of rainfall and elevation of the lake surface were taken on a daily basis by U.S. Army Corps of Engineers personnel at the Falls Lake Management Center.

Statistical Analyses. A time series analysis was used to determine the time lag between the rise of Falls Lake in mid-August and production of *An. quadrimaculatus* and *Cx. erraticus* larvae and adults. The untransformed basin-wide average number of larvae per dip and weekly mean number of females collected in resting shelters from the first week in August to the first week in October were correlated with lake level data recorded on earlier dates. On each iteration, a varying number of days was subtracted from each date on which adults or larvae were sampled, the data sets were merged (by date), and Pearson product-moment correlation analyses were carried out. This time lag procedure was repeated until the correlation coefficient of the average per dip or abundance of females and the lake level profile was maximized. The number of days needed for the best fit (highest r value) represented the amount of time between when the lake rose and the populations of larvae and adults reached peak levels.

Results

Seasonal Abundance of Adult Mosquitoes. Approximately 95% of the 48,670 mosquitoes collected in the resting shelters were *An. quadrimaculatus* and *Cx. erraticus.* In total, 7,009 females and 9,344 males of *An. quadrimaculatus* were aspirated from 14 shelters during weekly collections from 1 May to 3 December in 1985. In 1986 in total, 9,228 females and 11,657 males of *An. quadrimaculatus* were aspirated from 16 shelters during weekly collections from 1 May to

4 December. The mean number of *An. quadrimaculatus* females per shelter ranged from a low of 2.4 on 16 July when lake elevation was low to a high of 109.3 on 24 September after the lake level increased in 1985, and from 1.3 on 21 August to 67.5 on 25 September 1986 (Fig. 2). The abundance of females generally declined in July and populations were depressed into August in coincidence with the decline in the level of Falls Lake (Fig. 2). The lake level rose dramatically in late August following several days of intense rainfall. A second peak of abundance of females occurred in late September following the rise in Falls Lake. The patterns of seasonal abundance of *An. quadrimaculatus* females and males were similar. Mean numbers of males collected per shelter ranged from 1.6 in 1985 on 21 May when the lake level was low to 137.0 on 24 September when the lake level rose; and 2.1 on 27 August to 74.9 on 1 October in 1986.

In total, 2,678 females and 772 males of *Cx. erraticus* were aspirated from shelters in 1985, and in 1986, 2,517 females and 600 males were collected. The mean numbers of female *Cx. erraticus* collected from resting shelters ranged from a low of 1.1 on 28 May to a high of 18.4 on 27 August during 1985, and from 0.11 on 19 and 26 November to 13.4 on 25 September in 1986 (Fig. 3). Peaks of abundance in the population of females occurred on 27 August (18.4 females), 10 September (16.7 females), and 24 September (13.7 females) during 1985, and on 16 July (12.5 females), 6 August (10.8 females), 25 September (13.4 females), and 15 October (8.1 females) during 1986. The seasonal pattern of occurrence of males fluctuated more than that of females and it was not congruent with the pattern found for females. Mean numbers of males per resting shelter fluctuated during 1985 from a low of 0 on 4 June–2 July to a high of 9.3 on 22 July, and during 1986 from a low of 0 on 7 May and 19 November to a high of 3.9 males on 22 October.

Seasonal Abundance and Use of Habitat of Mosquito Larvae. The seasonal abundances of *An. quadrimaculatus* and *Cx. erraticus* collected in all habitats combined are presented in Figs. 2 and 3. *An. quadrimaculatus* exhibited vernal and autumnal peaks during both years. Larvae were absent for 2 wk in August of both years coincident with the lowest lake levels. In contrast to *An. quadrimaculatus, Cx. erraticus* did not exhibit a consistent pattern in the occurrence of larvae for the 2 yr (Fig. 3). Larval abundance was greatest in July 1985 (0.51 larvae per dip), then fluctuated at lower levels (0.0–0.071 larvae per dip) during the period of high lake level in September–October. In 1986, populations of *Cx. erraticus* larvae reached peak levels during late August (0.36 larvae per dip) when the lake elevation was lowest.

Although larval abundance for each species in the three habitats varied slightly between years, some trends in the use of habitat are apparent (Fig. 4). In 1985, *An. quadrimaculatus* was produced along creek edges only in the spring and early summer. Larval abundance increased markedly in the fall in the flood plain and lake edge habitats. In 1986, similar patterns of larval occurrence and abundance for *An. quadrimaculatus* larvae were observed except that the creek edge habitat was relatively less productive and the flood plain habitat relatively more productive in the late spring and summer. In 1985, *Cx. erraticus* larvae were abundant in vegetation along the lake edge in the spring; however, small numbers of larvae were collected thereafter (Fig. 4). The creek edge site was most productive in early summer and larval populations peaked in midsummer coincident with a decrease in production of larvae in lake edge habitats and the decline in elevation of Falls Lake. Flood plain habitats were moderately productive in the spring (0.28 larvae per dip) but populations declined in midsummer and no larvae were collected after September. A similar pattern of occurrence and abundance for *Cx. erraticus* larvae was observed in 1986 (Fig. 4); however, lake edge habitats were less productive and the creek edge habitat was more productive relative to 1985.

Effect of Seasonal Changes in the Level of Falls Lake on Mosquito Production. Production of *An. quadrimaculatus* increased following the rise of Falls Lake. In 1985, the larval population peaked ≈30 d after Falls Lake reached its peak (Table 1). The population of females reached peak numbers only 14 d following the rise in Falls Lake. In 1986, the same pattern was repeated with larval and adult populations reaching maximal levels in 30 and 26 d, respectively, after the level of Falls Lake peaked. Seasonal changes in the lake level appeared to affect the production of *Cx. erraticus* in a manner that was markedly different than for *An. quadrimaculatus*. Results of correlation analyses (Table 1) suggest that production of *Cx. erraticus* larvae and adults was negatively affected by changes in the level of Falls Lake during late summer. Even though correlation coefficients were generally only marginally significant ($0.10 \leq P \geq 0.013$), all of the coefficients had a negative sign indicating an inverse relationship between mosquito production and the level of Falls Lake.

Seasonal Changes in the Gonotrophic Status of *An. quadrimaculatus*. In 1985, collections of mosquitoes from resting shelters were initiated in mid-May. The percentage of blood-engorged females in collections reached peak levels in late June (33%) and again in early August (27%) (Fig. 2). Blood feeding declined in October and had ceased by the beginning of November. In March 1986, all 27 females taken from 2 of 16 shelters were unfed. Subsequently, in April when routine sampling was initiated, 1 of 53 females col-

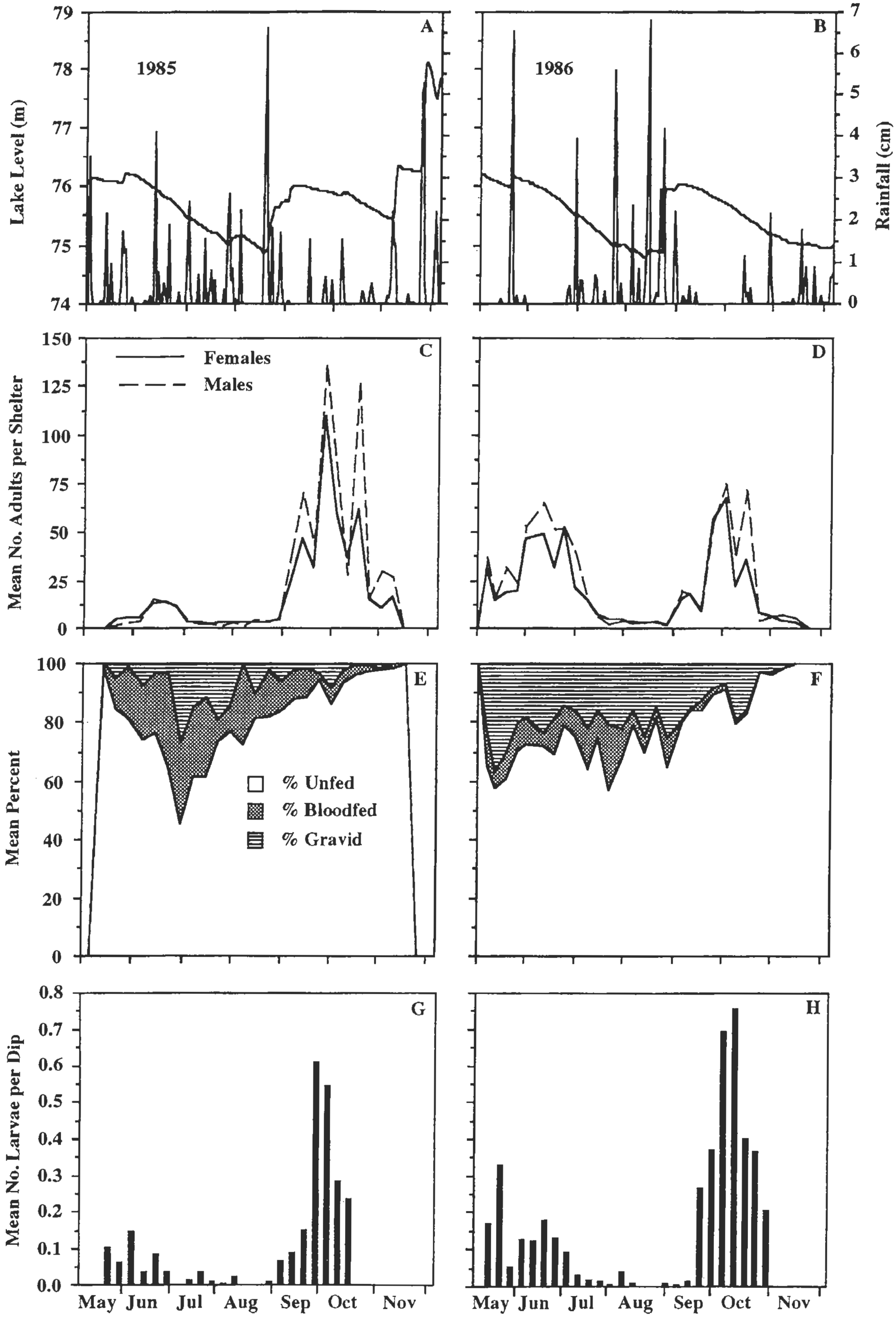

Fig. 2. Rainfall and lake level profiles at Falls Lake Management Center in 1985 (A.) and 1986 (B). Weekly mean number of *An. quadrimaculatus* adults collected in resting shelters in 1985 (C) and 1986 (D). Gonotrophic status of females collected in resting shelters in 1985 (E) and 1986 (F). Weekly mean number of larvae collected per dip in 1985 (G) and 1986 (H).

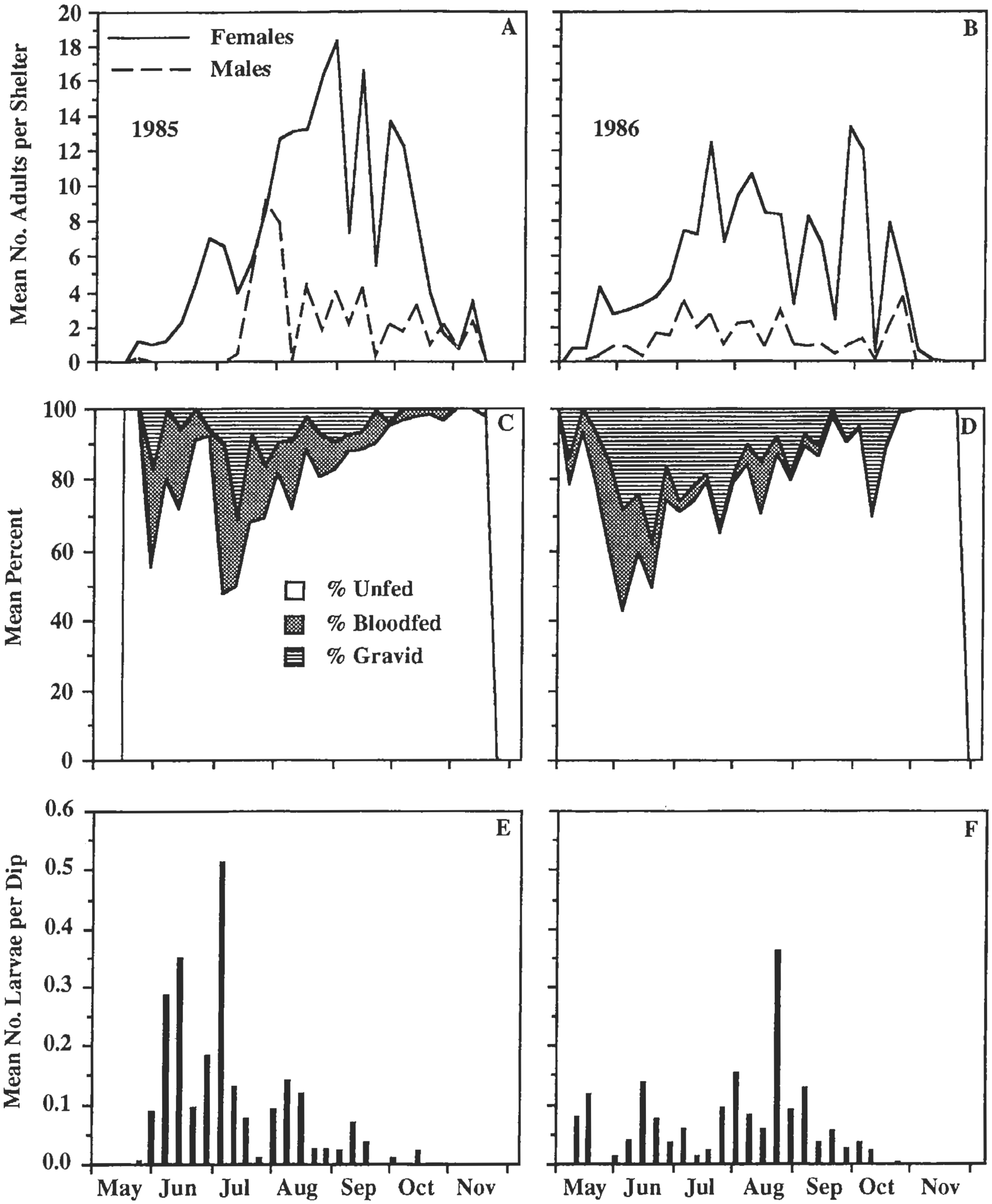

Fig. 3. Weekly mean number of *Cx. erraticus* adults collected in resting shelters in 1985 (A) and 1986 (B). Gonotrophic status of females collected in resting shelters in 1985 (C) and 1986 (D). Weekly mean number of larvae collected per dip in 1985 (E) and 1986 (F).

lected (1.9%) was engorged with blood. Blood-feeding activity peaked in mid-July when 23% of the females were found to be engorged. Blood feeding declined in September and October and ceased in early November.

Seasonal Changes in the Gonotrophic Status of *Cx. erraticus*. The population of *Cx. erraticus* became gonotrophically active earlier in the season than *An. quadrimaculatus*. In 1985, a large proportion (≈25%) of females in the first collec-

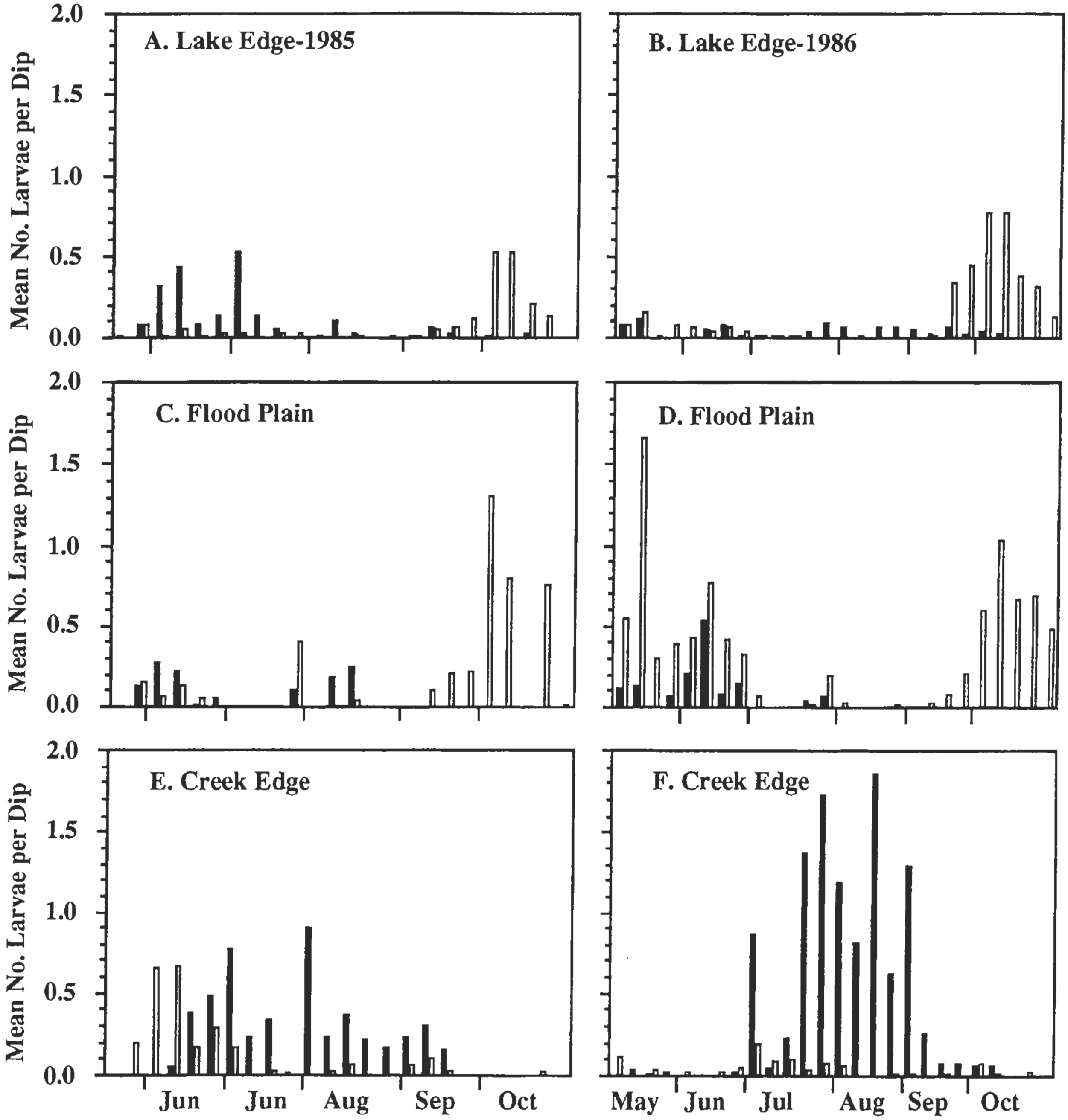

Fig. 4. Abundance of *Anopheles quadrimaculatus* (□) and *Culex erraticus* (■) larvae in lake edge, flood plain, and creek edge habitats in the Falls Lake basin in 1985 and 1986.

tion in mid-May contained a blood meal (Fig. 3). Blood feeding peaked in late June (40%), declined in September, and by November most females (>96%) were unfed. In 1986, 4 of 42 females (10%) in the first collection in mid-April had taken a blood meal (Fig. 2). Blood feeding peaked in late May (27%) and again in early August (15%). Blood-fed mosquitoes were not collected after late September.

Hosts of Mosquitoes. General screening assays were conducted on 1,289 blood-fed mosquitoes and 77.9% reacted with screening antisera (Table 2). Approximately 90% of the nonreactive blood-fed mosquitoes were collected in 1985. Seasonal changes in the use of hosts and multiple feedings by mosquitoes were not detected.

Anopheles quadrimaculatus fed on 11 mammalian species, and the largest percentage (25.1%) of blood meals were taken from white-tailed deer. Few *An. quadrimaculatus* (1.1%) fed on birds (Table 2). *Cx. erraticus* exhibited the more diverse feeding pattern with blood meals identified from 17 species or groups of hosts (Table 2). White-tailed deer (13.2%), turtles (6.6%), and columbiform birds (11.2%) were the most commonly used hosts.

Table 1. Correlation of abundance of *An. quadrimaculatus* and *Cx. erraticus* with the level of Falls Lake from the first week in August to the second week in October

Parameter	Maximum r value ($P > r$)		Days lagged	
	1985	1986	1985	1986
Anopheles quadrimaculatus				
Mean no. females per shelter	0.79 (0.012)	0.81 (0.0083)	14	26
Mean no. larvae per dip	0.90 (0.0023)	0.86 (0.0016)	30	36
Culex erraticus				
Mean no. females per shelter	−0.67 (0.062)	−0.58 (0.10)	10	42
Mean no. larvae per dip	−0.82 (0.013)	−0.58 (0.078)	0	18

Discussion

In the southeastern United States, *Anopheles quadrimaculatus* primarily overwinters as inseminated, nulliparous females (Barber et al. 1924, Balfour 1928, Boyd & Weathersbee 1929, Hinman & Hurlburt 1940, Hess & Crowell 1949, Zukel 1949, Hitchcock 1968). *An. quadrimaculatus* appeared to terminate host seeking in Falls Lake by October. In the fall, no blood-engorged mosquitoes were collected after the end of October. Although shelters at Falls Lake were checked during winter on a monthly basis, adults were seldom collected; the few adults that were collected were unfed. The resting shelters used at Falls Lake were probably summer diurnal resting places rather than winter hibernation sites because they would not protect mosquitoes from low winter temperatures. In coastal North Carolina, Balfour (1928) and Boyd & Weathersbee (1929) reported that generally only a few blood-fed specimens were collected in winter but that during warm periods, mosquitoes engorged with fresh blood were found, indicating that females had left hibernacula to seek hosts. Digestion of blood and development of ovaries progressed slowly throughout the winter, and oviposition occurred as early as January or February. If the biology of overwintering females at Falls Lake is similar, it is likely that adults collected in resting shelters in May were not overwintering females but their progeny.

Table 2. Hosts of *An. quadrimaculatus* and *Cx. erraticus* collected in resting shelters in the Falls Lake basin during 1985 and 1986

Hosts	*Anopheles quadrimaculatus*	*Culex erraticus*
Total mammal	770 [98.6][a]	111 [49.3]
Horse	181 (19.2)[b]	0 —
Cow	33 (3.5)	2 (0.6)
Deer	236 (25.1)	46 (13.2)
Cow or deer	44 (4.7)	6 (1.7)
Pig	20 (2.1)	6 (1.7)
Fox or dog	15 (1.6)	11 (3.2)
Rabbit	4 (0.4)	1 (0.3)
Opossum	2 (0.2)	0 —
Raccoon	3 (0.3)	0 —
Cat	1 (0.1)	1 (0.3)
Rodent	1 (0.1)	1 (0.3)
Human	2 (0.2)	6 (1.7)
Unidentified mammal	228 (24.2)	31 (8.9)
Total reptile or amphibian	2 [0.3]	45 [20.0]
Turtle	1 (0.1)	23 (6.6)
Snake	0 —	11 (3.2)
Toad	0 —	3 (0.9)
Bullfrog	0 —	1 (0.3)
Unidentified reptile or amphibian	1 (0.1)	7 (2.0)
Total bird	9 [1.1]	69 [30.7]
Chicken	4 (0.4)	0 —
Turkey	1 (0.1)	1 (0.3)
Passeriformes	0 —	10 (2.9)
Columbiformes	1 (0.1)	39 (11.2)
Strigiformes	1 (0.1)	1 (0.3)
Unidentified bird	2 (0.2)	18 (5.2)
Unidentified host	160 —	123 —
Total no. tested	941 —	348 —

Percentages in brackets are those of the total number identified for the mosquito species; percentages in parentheses are those feeding on hosts.

In the spring, blood feeding by *Cx. erraticus* was initiated earlier than by *An. quadrimaculatus*. The first collection of *Cx. erraticus* in both years of our investigation contained high proportions of blood-fed and gravid mosquitoes. In the fall, blood feeding ceased in the middle of October in 1985 and in the middle of September in 1986. Blood-engorged *Cx. erraticus* were not collected during winter. Eldridge (1987) reviewed the overwintering of *Culex* mosquitoes. No information is available for *Cx. erraticus;* however, most *Culex* overwinter as inseminated females. Females usually cease blood feeding in the fall and enter facultative diapause (Bates 1949, Blackmore & Dow 1962, Bellamy & Reeves 1963, Clements 1963, Spielman & Wong 1973).

The seasonal occurrence and abundance of *An. quadrimaculatus* varies with its distribution. Bradley & Fritz (1945) found that between the 12.8 and 15.6°C isotherms, which includes most of North Carolina, adult populations of *An. quadrimaculatus* increased in early May, peaked in August, and declined to a low level in early December. Similar results were reported by Love & Goodwin (1961) for southwestern Georgia. *An. quadrimaculatus* in Falls Lake exhibited bimodal peaks of abundance with largest numbers of both larvae and adults present during September and October.

The population dynamics of *An. quadrimaculatus* in 1985 and 1986 were associated with seasonal changes in the level of Falls Lake. Lake level fluctuations were influenced by evaporation, man-regulated discharge and, more important, rainfall. The abundance of *An. quadrimaculatus* increased notably in late summer following a 1-m rise in the level of the reservoir caused by heavy rainfall that occurred during the middle of August (Fig. 2). A 1-m rise in the lake level flooded the lake shoreline and flood plains and created suitable habitat for the production of *An. quadrimaculatus*. It is well established that anopheline mosquitoes breed in association with living plants or plant parts (flotage) (Rozeboom & Hess 1944, Penfound et al. 1945, Furlow & Hays 1972, Hall 1972). An association between seasonal water levels, plant growth, and production of *An. quadrimaculatus* females has been observed on TVA reservoirs (TVA 1947). In these reservoirs, spring and early summer recession of the reservoir levels exposed the lake margins to plant invasion. When reservoirs were refilled, excessive mosquito production occurred. Similar results were found during our 2-yr investigation at Falls Lake.

The autumnal rise in the level of Falls Lake enhanced production of both *An. quadrimaculatus* larvae and adults. Correlation analyses suggested that population peaks for adults occurred before larvae. An increase in adults should be preceded by an increase in abundance of larvae. No explanation can be provided for this anomaly. Contrasting results were obtained for *Cx. erraticus*. Production of larvae and adults were negatively correlated with lake level. Apparently, the recession of Falls Lake increased breeding sites for *Cx. erraticus* in creeks. However, because only one flood plain and creek edge habitat was sampled in our investigation, the relative abundances of *Cx. erraticus* and *An. quadrimaculatus* larvae in these two habitats should be studied further at additional sites so that the observed seasonal profiles can be verified.

Numerous host-feeding investigations have been conducted in the eastern and southern United States (see Tempelis [1975] and Washino & Tempelis [1983] for reviews). Results of our study conducted in the northeastern Piedmont of North Carolina are similar to results obtained in other locales. Earlier studies have shown that mammals are the primary hosts of *An. quadrimaculatus*. Tempelis (1975) found that horses and "bovines" (cow–deer) were most commonly used as hosts. Likewise in our study, large mammals such as cow, deer, and horses were fed upon by *An. quadrimaculatus*. Bloodmeal sources for sympatric sibling species A and B of *An. quadrimaculatus* in an area of Mississippi were recently reported by Apperson & Lanzaro (1991). Females of both sibling species predominantly had fed on white-tailed deer. A single sample ($n = 119$) of the population of *An. quadrimaculatus* at Falls Lake comprised species A (90.6%) and B (9.2%) (Seawright et al. 1992). In both studies, the large percentage of deer blood meals reported probably reflected the local high abundance of this host.

Culex erraticus exhibited catholic feeding habits at Falls Lake. Mammalian, reptilian, amphibian, and avian hosts were fed upon with no single vertebrate class dominating. Edman (1979) in Florida and Tempelis (1975) in Illinois and Minnesota reported that birds were primary hosts for *Cx. erraticus*. Irby & Apperson (1988) found *Cx. erraticus* in the Coastal Plain of North Carolina used a broad range of hosts including mammals, reptiles, amphibians, and birds.

During our investigation, very little human activity occurred in proximity to Falls Lake, which may explain the relatively few human blood meals identified. Only eight human blood meals were detected for *An. quadrimaculatus* and *Cx. erraticus*. However, as human activity increases around the lake, humans will likely be used as hosts more frequently by the mosquito population produced in the Falls Lake basin. Although *Cx. erraticus* is not recognized as an important nuisance species, its relative abundance at Falls Lake and similar reservoirs in combination with its opportunistic feeding habits suggest that it may eventually achieve this status.

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References Cited

Apperson, C. S. & G. C. Lanzaro. 1991. Comparison of host-feeding patterns between *Anopheles quadrimaculatus* sibling species A and B. J. Am. Mosq. Control Assoc. 7: 507–508.

Balfour, M. C. 1928. Studies on the bionomics on North American anophelines. 2. Winter activities of anophelines in coastal North Carolina (36° N Lat.). Am. J. Hyg. 8: 68–76.

Barber, M. C., W.H.W. Komp & T. B. Hayne. 1924. Some observations on the winter activities of *Anopheles* in southern United States. Pub. Health Rep. 39: 231–246.

Bates, M. 1949. The natural history of mosquitoes. Macmillan, New York.

Bellamy, R. E. & W. E. Reeves. 1963. The winter biology of *Culex tarsalis* in Kern County, California. Ann. Entomol. Soc. Am. 56: 314–323.

Blackmore, J. E. & R. P. Dow. 1962. Nulliparity in summer and fall populations of *Culex tarsalis* Coq. Mosq. News 22: 291–294.

Boyd, M. F. 1927. Studies on the bionomics of North American anophelines. I. The number of annual broods of *A. quadrimaculatus*. Am. J. Hyg. 7: 264–275.

Boyd, M. F. & A. A. Weathersbee. 1929. Studies on the bionomics of North American anophelines. V. Winter activities of anophelines imagines in coastal North Carolina (36° N Lat.). Am. J. Hyg. 9: 682–694.

Bradley, G. H. & R. F. Fritz. 1945. Observations on seasonal occurrence and abundance of *Anopheles quadrimaculatus* Say. J. Natl. Malaria Soc. 4: 251–262.

Carter, H. R. 1915. Impounded waters. Their effect on the prevalence of malaria—survey at Blewetts Falls. Publ. Health Rep. 30: 15–33.

Clements, A. N. 1963. The physiology of mosquitoes. Pergamon, London.

Edman, J. D. 1979. Host-feeding patterns of Florida mosquitoes (Diptera: Culicidae). VI. *Culex (Melanoconion).* J. Med. Entomol. 15: 521–525.

Eldridge, B. F. 1987. Diapause and related phenomenon in *Culex* mosquitoes: their relation to arbovirus disease ecology, pp. 1–28. *In* Harris, K. F. [ed.], Current topics in vector research, vol. 4. Springer, New York.

Furlow, B. M. & K. L. Hays. 1972. Some influences of aquatic vegetation on the species and numbers of Culicidae (Diptera) in small pools of water. Mosq. News 32: 595–599.

Gage, E. H. 1925. Studies of impounded waters in relation to malaria. The trend of malaria in Horse Creek Valley, Aiken County, SC. Publ. Health Rep. 49: 2011–2219.

Gartrell, F. E., J. C. Cooney, G. P. Chambers & R. H. Brooks. 1981. TVA mosquito control 1934–1980—experience and current program trends and developments. Mosq. News 41: 302–322.

Hall, J. F. 1972. The influence of plants on *Anopheles* breeding. Am. J. Trop. Med. Hyg. 21: 787–794.

Hess, A. D. & R. L. Crowell. 1949. Seasonal history of *Anopheles quadrimaculatus* in the Tennessee Valley. J. Natl. Malaria Soc. 8: 159–170.

Hinman, E. H. & H. S. Hurlburt. 1940. A study of winter activities and hibernation of *Anopheles quadrimaculatus* in the Tennessee Valley. Am. J. Trop. Med. Hyg. 20: 431–446.

Hitchcock, J. C. 1968. Age composition of a natural population of *Anopheles quadrimaculatus* Say (Diptera: Culicidae) in Maryland, U.S.A. J. Med. Entomol. 5: 125–134.

Horsfall, W. R. & A. P. Morris. 1952. Surface conditions limiting larval sites of certain marsh mosquitoes. Ann. Entomol. Soc. Am. 45: 492–498.

Irby, W. S. & C. S. Apperson. 1988. Hosts of mosquitoes in the coastal plain of North Carolina. J. Med. Entomol. 25: 85–93.

Love, G. J. & M. H. Goodwin, Jr. 1961. Notes on the bionomics and seasonal occurrence of mosquitoes in southwestern Georgia. Mosq. News 21: 195–215.

Morris, C. D. 1981. A structural and operational analysis of diurnal resting structures for mosquitoes (Diptera: Culicidae). J. Med. Entomol. 18: 419–424.

Penfound, W. T., T. F. Hall & A. D. Hess. 1945. The spring phenology of plants in and around the reservoirs in North Alabama with particular reference to malaria control. Ecology 26: 332–352.

Rozeboom, L. E. & A. D. Hess. 1944. The relation of the intersection line to the production of *Anopheles quadrimaculatus.* J. Natl. Malaria Soc. 3: 169–179.

Seawright, J. A., P. E. Kaiser, S. K. Narang, K. J. Tennessen & S. E. Mitchell. 1992. Distribution of sibling species A, B, C and D of the *Anopheles quadrimaculatus* complex. J. Agric. Entomol. 9: 289–300.

Spielman, A. & J. Wong. 1973. Studies on autogeny in natural populations of *Culex pipiens.* III. Midsummer preparation for hibernation in anautogenous populations. J. Med. Entomol. 10: 319–324.

Tempelis, C. H. 1975. Host-feeding patterns of mosquitoes, with a review of advances in analysis of blood meals by serology. J. Med. Entomol. 11: 635–653.

TVA (Tennessee Valley Authority). 1947. Malaria control on impounded waters. U.S. Government Printing Office, Washington, DC.

Washino, R. K. & C. H. Tempelis. 1983. Mosquito host bloodmeal identification: methodology and data analysis. Annu. Rev. Entomol. 28: 179–201.

Zukel, J. W. 1949. A winter study of *Anopheles* mosquitoes in southwestern Georgia with notes on some culicine species. J. Natl. Malaria Soc. 8: 224–233.

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