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Species Composition and Life Histories of Aquatic Insects in a Lowland Sonoran Desert Stream

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ABSTRACT: Ninety-nine taxa of aquatic insects and a total 104 macroinvertebrate taxa were collected in Sycamore Creek, Arizona, from July 1977 to November 1979. The fauna is primarily composed of organisms restricted to the American Southwest, although many widespread Nearctic taxa are also present. Life histories of 17 taxa were examined with emphasis on total developmental time (egg to adult), reproductive period and dormancy. Ephemeroptera, small Diptera and the corixid *Graptocorixa ser-rulata* developed rapidly (1-3 weeks) and reproduced continuously. Aquatic beetles (Dytiscidae and Hydrophilidae) developed in 4-8 weeks and reproduced only in spring and after summer rains. Two Trichoptera species required 6-7 weeks for development and reproduced continuously. Degree-day developmental rates (ca. 1200) were similar for some desert and temperate species. Dormant stages were restricted to stoneflies (egg diapause) and tabanids (larval diapause). Drought and flooding markedly influenced life histories. Adaptations to drought are habitat selection by ovipositing adults and rapid development. Adaptations to floods are behavioral avoidance, rapid development and seasonal reproduction. Floods also contribute to the rarity of dormancy, thus aerial adults become the life stage resistant to disturbance. Floods, which do not occur in temporary lentic systems, are an important selective pressure in temporary lotic systems.

INTRODUCTION

Little is known of life histories of aquatic insects in the American Southwest. In large part, this results from gaps in taxonomic information on many important groups. A number of recent studies have closed these gaps and provided an essential base for life history considerations (Allen, 1967, 1978; Burger, 1977; Gordon, 1974; Gundersen, 1977; Kilgore and Allen, 1973; Menke, 1978; Morihara and McCafferty, 1979; Van Tassell, 1963; Wiggins, 1977; Zimmerman and Smith, 1975). This paper describes species composition and life history characteristics of aquatic insects in a lowland Sonoran Desert stream, Sycamore Creek, Arizona. Objectives include a compilation of species present in the watershed along with their geographical origins and distributions, description of basic life history characteristics (developmental times, reproductive periods and dormant stages) and effects of hydrologic extremes on the latter. At present, the only published species lists for lowland Sonoran Desert streams are those of Bruns and Minckley (1980) and Lewis and Burraychak (1979). Previous life history studies of desert aquatic insects include Burger (1977) and Smith (1975) on Tabanidae (Diptera) and Belostomatidae (Hemiptera), respectively. For other major groups, such as Ephemeroptera, Trichoptera and Plecoptera, no life history information has been published.

Life histories of 17 taxa, including a stonefly, four mayflies, two caddisflies, four beetles, a corixid and five dipterans, were examined in detail. These organisms possess characteristics markedly different from their counterparts in mesic streams, in particular, continuous reproduction, extremely rapid development and lack of dormant stages. Overall, the life cycles of these insects have important community and ecosystem consequences, demonstrate the significance of hydrologic extremes as selec-

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tive pressures in desert lotic habitats and, in general, indicate that adaptations of aquatic organisms are shaped by predictability of climatic events and the nature of channel processes.

STUDY AREA

Sycamore Creek (33° 45' N, 111° 30' W) originates in the Mazatzal Mountains of central Arizona (elevation 2160 m) and flows 65 km to enter the Verde River (430 m elevation). Climate of the watershed is arid. Mean annual precipitation is 51 cm at midbasin and 23 cm at the Verde River; 55% occurs in winter (November through April). Riparian vegetation consists of shrubs and scattered large trees, and most wider parts of the channel are unshaded (Campbell and Green, 1968). Basin land use is predominately livestock grazing and low-density recreation.

For purposes of this report, a flood was defined as discharge which scoured substrates (mainly sands and gravels at lower elevations) and disrupted the biota of Sycamore Creek. Floods occurred when discharge exceeded 1.0 m³/s and occur ca. five times a year, although this number may vary from 1-16 (Thomsen and Schumann, 1968). Winter floods affect the entire basin, resulting in sustained high flows for days to weeks after precipitation. Summer floods occur from mid-July to early September and affect variable portions of the watershed, depending upon the location of the thunderstorm (Deacon and Minckley, 1974). Little precipitation occurs in spring (May and June).

Water temperature of Sycamore Creek rarely exceeded the range of 10-30 C, and large diel and microhabitat differences masked seasonal differences. Representative diel extremes in the main channel, by selected month, were: February, 10-15 C; April, 11-21 C; June, 17-25 C; August, 22-28 C, and November, 12-17 C. Instantaneous differences between microhabitats, such as main channel vs. side pool, can be as great as 6-12 C. Diel extremes in air temperature, in the same months, are: February, 6-20 C; April, 11-28 C; June, 19-38 C; August, 24-39 C, and November, 9-24 C (Green and Sellers, 1964; data from site 12 km W of Sycamore Creek).

METHODS

Benthic aquatic insects were collected at weekly or biweekly intervals from July 1977 to December 1979 with core samplers (325 cm² and 80 cm²) and dipnets (270 μm mesh). Principal study sites were at elevations from 550-1040 m on the main stem. Occasional collections were made from small tributaries and various springs throughout the watershed. These collections and light trap samples supplied data on species composition and reproductive periods.

Developmental rates were obtained by one or more of three methods for each taxon:

(1) Laboratory rearings were conducted in aerated, 19-liter aquaria with sand-gravel substrates; pH was adjusted to 7.5 and conductivity to 200-400 μS cm⁻¹ (values typical of Sycamore Creek). One-half of the total water volume was changed weekly. All rearings were conducted at water temperatures of 22 ± 2 C with natural photoperiods. Herbivores were fed a mixture of algae and detritus obtained from laboratory cultures or the stream and was inspected before use to insure that no insect eggs or larvae were present. Predators were fed Tetra-Min[®] commercial fish food for the first few days after hatching and later fed small dipteran and mayfly larvae. *Tropisternus ellipticus* larvae were reared in styrofoam cups (one larva per cup) containing stream water and filamentous algae as substrate. They received dipteran larvae as food three or more times daily (see Young, 1958).

(2) Field rearings were conducted in trays that allowed adult colonization only. Plywood boxes, 16 cm deep X 28 cm wide X 60 cm long with 60 μm nylon mesh at each end, were filled with clean sand and gravel to a depth of 5 cm and placed in the stream for 6-9 days. Immature insects collected after this period were sorted by taxon and size. Size classes of larvae were based on total length (mm) excluding cerci. Because exact

oviposition time was not known, tray data indicate maximum time for development to a given size.

(3) Approximate developmental times for several beetles were taken as the time difference between initial immigration of gravid females into ephemeral tributaries after flooding and first emergence of teneral. Because many taxa did not reproduce synchronously, size class distributions from benthic samples were unreliable as indicators of developmental rate.

RESULTS AND DISCUSSION

Species composition and geographical distributions. — Ninety-nine taxa of aquatic insects were recorded in Sycamore Creek (Table 1). This is an obvious underestimate because of the large number of Diptera that could not be identified to species. Species richness is comparable to other streams in North American deserts, e.g., 69 insect taxa were found in Piceance Creek, Colorado (Great Basin Desert; Gray and Ward, 1979); 56 taxa in Aravaipa Creek, Arizona (Sonoran Desert; Bruns and Minckley, 1980); and 48 taxa in Pinto Creek, Arizona (Sonoran Desert; Lewis and Burraychak, 1979).

The ranges of many species in Sycamore Creek are restricted to the arid American Southwest (Table 2). The only species in the fauna that is endemic to Arizona is *Mesocapnia arizonensis* (Baumann and Gaufin, 1970). Southwestern species are largely derived from genera with Neotropical centers of speciation, e.g., the mayfly genera *Leptohyphes*, *Tricorythodes* and *Thraulodes* (Allen, 1978; Allen and Brusca, 1978; Edmunds et al., 1976); the caddisfly genera *Chimarra*, *Culoptila*, *Helicopsyche* and *Marilia* (Wiggins, 1977); the beetles *Deronectes* spp. (Zimmerman and Smith, 1975), and the hemipteran *Abedus herberti* (Menke, 1960). A relatively large part of the fauna, however, is comprised of species with much larger North American (Nearctic) ranges, e.g., *Helicopsyche borealis*, *Tropisternus ellipticus*, *Agabus seriatus*, *Deronectes striatellus*, *Corydalis cornutus*, *Trichocorixa reticulata*, all *Simulium* species, and probably all the Odonata. Thus the fauna may be characterized as a combination of Neotropical and Nearctic elements.

Life histories. — Plecoptera. Only two stonefly species were collected in the Sycamore Creek watershed, *Mesocapnia arizonensis* and an undetermined taeniopterygid (only one adult of which was collected). *Mesocapnia arizonensis* was present only in winter. Nymphs were initially abundant in high elevation tributaries after winter rains and later became abundant at lower main channel sites, presumably due to drift. Total developmental time was not determined.

Other capniid species are known to possess a nymphal diapause (Hynes, 1976), but *Mesocapnia arizonensis* appears to have egg diapause. In April 1979, a cluster of ca. 250 *M. arizonensis* eggs were collected. Some eggs hatched in the laboratory but hatching abruptly ceased several days later. This cessation corresponded to a decline in numbers of nymphs and adults in the field.

Field data suggested that hatching ceased when maximum stream temperature exceeded 20 C. Egg diapause was also suggested by the absence of nymphs within stream substrates after April. Substrates down to 20-cm depth are the typical habitat for diapausing capniid nymphs (Harper and Hynes, 1972; Hynes, 1976).

Ephemeroptera. Mayflies of Sycamore Creek were alike in life history traits in that four species examined possessed rapid development (egg to adult in 8-14 days), continuous reproduction and no dormancy (Table 2). *Baetis quilleri* and *Callibaetis montanus* were reared in the laboratory and tray data were obtained for all four species.

Baetis quilleri eggs, obtained from reared adults, hatched in 1 or 2 days. Subimagos emerged in 9-11 days. Larvae with fully developed wing pads were present after 6 days at 17-25 C in trays. *Callibaetis montanus* subimagos emerged 13 days after larvae 1 mm in body length were placed in aquaria, and field rearings suggested an even shorter developmental time (Fig. 1). According to Berner (1959), eggs of *Callibaetis* species hatch immediately upon release by the female. Similar developmental times were found for *Leptohyphes packeri* and *Tricorythodes dimorphus* in trays (Fig. 1).

Adults of all four species were collected in each month. Continuous emergence has been noted for many other *Baetis* species in Florida (Berner, 1959).

These developmental rates are the most rapid yet known among the Ephemeroptera. The shortest developmental period previously reported is for *Paramerletus columbiae* (16-22 days), although that species has an egg diapause which lasts a year (Edmunds *et al.*; 1976). Hynes (1975) reported that *Centroptilum* sp. larvae developed in 18 days in a warm, intermittent river in southern Ghana. Sycamore Creek mayflies completed development in 180-310 deg-days (number of days times

TABLE 1.—List of aquatic macroinvertebrates collected in Sycamore Creek watershed, Arizona, July 1977-November 1979. Numbers in parentheses are total taxa in each order or group

Ephemeroptera (9)

Baetidae: *Baetis quilleri* Dodds, *B. insignificans* McDunnough, *Callibaetis montanus* Eaton, *Centroptilum* sp. Caenidae: *Caenis* sp., Leptophlebiidae: *Thraulodes speciosus* Traver, Siphonuridae: *Siphonurus* sp., Tricorythidae: *Leptohyphes packeri* Allen, *Tricorythodes dimorphus* Allen

Plecoptera (2)

Capniidae: *Mesocapnia arizonensis* (Baumann and Gaufin), Taeniopterygidae: undetermined sp.

Trichoptera (11)

Glossosomatidae: *Culoptila cantha* (Ross), Helicopsychidae: *Helicopsyche mexicana* Banks, *H. borealis* Hagen, *Cheumatopsyche arizonensis* (Ling), *Hydropsyche venada* (?) Ross, Hydroptilidae: *Ochrotrichia* sp., Limnephilidae: *Limnephilus* sp., Odontoceridae: *Marilia* (2 spp.), Philopotamidae: *Chimarra angustipennis* Banks, Polycentropodidae: *Polycentropus halidus* Milne

Lepidoptera (1)

Pyralidae: *Paragyraetis confusialis* (Walker)

Coleoptera (31)

Dytiscidae: *Deronectes nebulosus* (Sharp), *D. aequinoctialis* (Clark), *D. striatellus* (LeConte), *D. yaquii* Zimmerman & Smith, *D. roffi* (Clark), *Laccophilus pictus coccinelloides* Regimbart, *L. maculosus shermani* Leech, *Thermonectus marmoratus* (Hope), *Agabus seriatus* (Crotch), *Dytiscus marginicollis* LeConte, *Hydroporus* (2 spp.) *Bidessus* sp., *Oreodytes* sp., *Rhantus* sp.

Hydrophilidae: *Tropisternus ellipticus* (LeConte), *Enochrus carinatus fucatus* (Horn), *E. piceus glabrus* Gundersen, *Hydrochara lineata* LeConte, *Berosus punctatissimus* LeConte, *B. exilis* LeConte, *Laccobius* sp., *Hydrobius* sp.

Dryopidae: *Helichus inmsi* Hinton, Elmidae: *Microcylloepus* sp., Gyrimidae: *Gyrinus* sp., *Dineutus* sp., Haliplidae: *Peltodytes* sp., *Haliplus* sp., Hydroscaphidae: *Hydroscapha natans* LeConte, Psephenidae: *Psephenus murvoshi* Brown

Hemiptera (10)

Belostomatidae: *Abedus herberti* Hidalgo, Corixidae: *Graptocorixa serrulata* (Uhler), *Hesperocorixa* sp., *Trichorixa reticulata* (Guerin-Meneville) Naucoridae: *Ambrysus occidentalis* LaRivers, Nepidae: *Ranatra* sp., Notonectidae: *Notonecta indica* L., *N. lobata* Hungerford, *N. undulata* Say, *Buenoa arizonis* Bare

Diptera (28)

Tipulidae: *Cryptolabis* sp. *Tipula* sp. Simuliidae: *Simulium arcticum* Malloch, *S. virgatum* Coquillett, *S. canadense* Hearle Ceratopogonidae: *Probezzia* sp., *Dasyhelea* sp., Culicidae: *Culiseta incidens* (Thomsen), Stratiomyiidae: *Euparyphus* sp., *Eulalia* sp., Tabanidae: *Tabanus dorsifer* Walker, Dolichopodidae: undetermined sp., Muscidae: undetermined sp., Ephydriidae: undetermined sp., Chironomidae: Tanypodinae (3 spp. Pentaneurini), Orthoclaadiinae (*Cricotopus* sp., *Brillia* sp., *Cardiocladius* sp., *Eukiefferiella* sp., *Corynoneura* sp.), Chironominae (*Dicrotendipes* sp. (= *Limnochironomus* sp.), *Paratendipes* sp., *Chironomus* sp., *Tribelos* sp., *Microtendipes* sp., *Micropsectra* sp., *Polypedilum* sp.)

Odonata (5)

Gomphidae: *Progomphus borealis* McLachlan *Ophiogomphus bison* Selys, Libellulidae: *Pantala hymenea* (Say), Calopterygidae: *Hetaerina* sp., Coenagrionidae: *Argia* sp.

Megaloptera (1)

Corydalidae: *Corydalus cornutus* L.

Noninsects (5)

Oligochaeta: Tubificidae, Tricladida: *Dugesia* sp., Hirudinea: undetermined sp., Gastropoda: *Physa virgata* Gould, Acari: undetermined sp.

mean daily water temperature), considerably less than the 1300 deg-days typical of many temperate species (Cummins, 1974).

Trichoptera. *Helicopsyche mexicana* is the most common helicopsychid in Arizona (Denning and Blicke, 1979) and was the most abundant caddisfly in Sycamore Creek. Egg clusters of this species hatched in 6 days after oviposition in the laboratory. Larval development required a mean of 33 days, and pupation a mean of 11 days. Total developmental time therefore averaged 50 days (1,100 deg-days).

A similar developmental time was found for the other laboratory-reared species, *Polycentropus halidus*. Hatching required a minimum of 6 days and continued for 4 weeks. Larval development averaged 32 days and pupation was 8 days for a mean total developmental time of 46 days (1000 deg-days). Although a filter-feeder, this species tolerated the absence of current. Numerous living larvae were collected in drying pools and beneath stranded algal mats in August.

Five species of caddisflies reproduced continuously, based on light trap and quantitative benthic samples (*Helicopsyche mexicana*, *Polycentropus halidus*, *Cheumatopsyche arizonensis* and two species of *Marilia*). Each species could potentially produce seven generations a year, since mean generation time was 7 weeks. Most caddisfly species have one or two generations (Wiggins, 1977). However, total deg-days per generation for the desert species (1000-1100) are only slightly less than that of temperate species (1300) (Cummins, 1974). Fremling (1960) recorded a developmental time of 51 days for *Cheumatopsyche campyla* Ross from the Mississippi River. Thus desert species are similar in developmental times to temperate species, and the greater number of potential generations for desert species may result from warm stream temperatures.

No diapause or other form of dormancy has been confirmed for any desert caddisfly. The eggs of *Helicopsyche mexicana* and *Polycentropus halidus* were not resistant to desiccation as reported for other caddisflies by Wiggins (1977). Neither eggs nor larvae survived more than a few days in the field after disappearance of surface water.

Life cycles of other caddisflies in Sycamore Creek could not be determined due to their limited occurrence. *Chimarra angustipennis*, *Culoptila cantha* and *Ochrotrichia* sp. were only present in summer at lower main channel sites. *Limnephilus* sp. was found only in winter in higher elevation tributaries. *Helicopsyche borealis* were collected only as adults.

Coleoptera. Thirty-one species of aquatic beetles were collected and these comprised a large part of the Sycamore Creek fauna (Table 1). Overall, beetles had

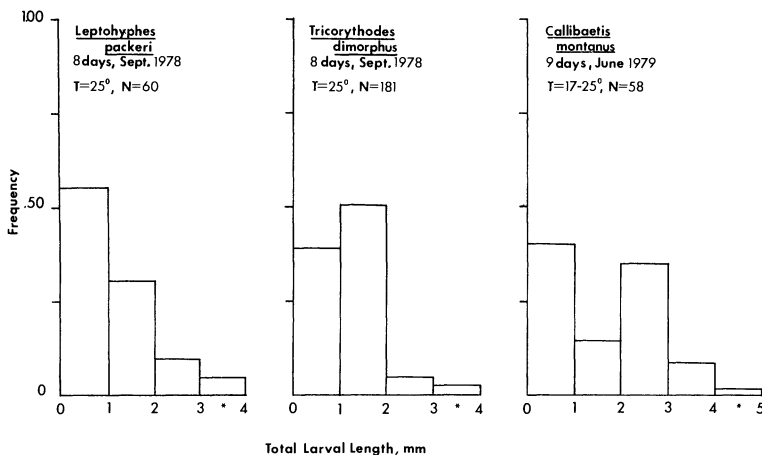


Fig. 1.—Size-class distributions of mayflies from colonization trays. Number of days is the time the trays were in the stream. Asterisk denotes size class of larvae with fully developed wing pads

TABLE 2. — Summary of life histories and geographic distributions of aquatic insects. Degree-day totals are number of days times mean daily water temperature

Species or Taxon	Total development (time)	Reproductive period	Diapause stages	Degree-days (approx.)	Potential generations per year	Distribution
Ephemeroptera						
<i>Baetis quilleri</i>	7-13 days	continuous	none	150-290	35	Primarily SW ¹
<i>Leptophyes packeri</i>	≥ 8 days	continuous	none	≥ 180	35	SW to Honduras
<i>Tricorythodes dimorphus</i>	≥ 8 days	continuous	none	≥ 180	35	SW
<i>Callibaetis montanus</i>	9-14 days	continuous	none	200-310	25	SW
Plecoptera						
<i>Mesocapnia arizonensis</i>	unknown	Dec.-April	egg	unknown	--	AZ
Trichoptera						
<i>Helicopsyche mexicana</i>	50 days	continuous	none	1100	7	SW
<i>Polycentropus halidus</i>	46 days	continuous	none	1000	7	SW
Coleoptera						
<i>Deronectes nebulosus</i>	4-5 weeks	March-July	none	500-700	1-2	SW
<i>Laccobius</i> sp.	4-5 weeks	April-July	none	500-700	2	unknown
<i>Tropisternus ellipticus</i>	53 ± 6 days	Sept.-Oct.	none	1100	2-3	western N. Am.
<i>Berosus punctatissimus</i>	5-6 weeks	March-Oct. May-June	none	800	1	western U.S.
Hemiptera						
<i>Grafitocoris serrulata</i>	21 days	continuous	none	460	17	OR, NV, AZ
<i>Abedus herberti</i> ²	80 days	continuous	none	1200	4+	SW
Diptera						
Chironomidae	9-16 days	continuous	none	200-350	35	unknown
<i>Probezzia</i> sp.	9-16 days	continuous	none	200-350	35	unknown
<i>Tabanus dorsifer</i> ³	1 year	July-August	larval	7000	1	SW

¹SW = southwestern U.S. (west Texas, New Mexico, Arizona, and southern California) and northwestern Mexico

²From Smith (1975)

³From Burger (1977)

developmental times of 4-8 weeks (Table 2), pronounced seasonal reproduction (Fig. 2) and no dormancy. Adults of all species were active throughout the year.

Forty *Tropisternus ellipticus* larvae were reared from eggs deposited July 1979. Eggs hatched in a maximum of 6 days, and all eggs within an egg case hatched simultaneously. Means and limits in days for duration of each stage were: 1st instar, 7 (5-9); 2nd instar, 11 (9-14); 3rd instar, 18 (17-79); and pupation, 11 (10-11). The total developmental time of 53 ± 6 is comparable to 45 days required by *T. ellipticus* in Oregon (Ryker, 1975).

In contrast to other groups, beetles exhibited pronounced seasonal reproduction (Fig. 2). Of 10 species for which data were obtained, six had peak reproduction in spring, and two in late summer. Peaks are defined here as periods when larval densities in quantitative samples exceeded one individual/m². These eight species had one (at most two) generations per year based on mean developmental time compared with length of reproductive period. *Laccobius* sp. was the only beetle to reproduce in both periods, with the second generation smaller than the first. Overwintering adult *Tropisternus ellipticus* reproduced throughout spring and early summer. First generation adults, which lacked parasitic fungi and scarred elytra characteristic of overwintering adults, reproduced after July. A third generation may occur in late summer. This reproductive pattern is similar to that reported by Riker (1975) for Oregon populations.

Hemiptera. Of 10 hemipterans in Sycamore Creek (Table 1), the two most common species were *Graptocorixa serrulata* and *Abedus herberti*. *Graptocorixa serrulata* was the primary invertebrate grazer of large filamentous algae (e.g., *Cladophora glomerata*), and *A. herberti* was the largest invertebrate predator in the stream.

Developmental time to first adult for *Graptocorixa serrulata* was 21 days (460 deg-days) (Sweeney and Schnack, 1977). Hatching through 3rd instar required 4-8 days with each stage about equal in duration. The 4th instar lasted 3 days, while the 5th required 12 days. Reproduction was continuous in main channel habitats; thus *G. serrulata* could potentially produce 17 generations per year.

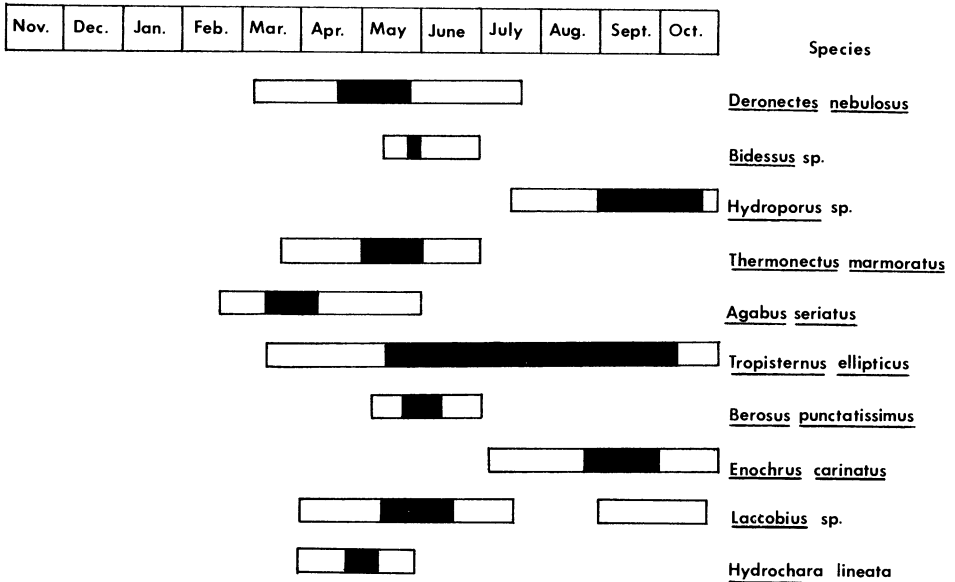


Fig. 2. — Larval periods of 10 beetle species. Bars indicate total period when larvae were present in mainstream sites; solid black bars depict peaks in larval numbers

Total developmental times reported for other corixids are considerably longer than that of *Graptocorixa serrulata*. Two species in a Mexican lake, *Krizousacorixa femorata* (= *Ahuautlea mexicana*) and *Trichocorisella mexicana*, require 5-6 weeks for development at 18 C, or 630-760 deg-days (Peters and Spurgeon, 1973; Peters and Ulbrich, 1973). Sweeney and Schnack (1977) found that *Sigara alternata* required 52 days (900 deg-days) for development in a Pennsylvania stream.

Smith (1975) reared *Abedus herberti* and determined that development averaged 80 days (1440 deg-days). One female, which lived for more than a year, produced four clutches of eggs. Thus *A. herberti* is the only known iteroparous aquatic insect in Sycamore Creek.

Diptera. Four chironomid species and one ceratopogonid were reared in the laboratory and these data were supplemented by field rearings (Fig. 3). Overall, life histories of these small dipterans were similar to those of mayflies. All developed rapidly, reproduced continuously and lacked dormant stages.

Chironomid eggs collected in trays were concentrated in the center of a gelatinous matrix, 1.0-1.2 mm in diam, each egg mass containing 25-50 eggs. Eggs hatched simultaneously in a maximum of 2 days, and larval development was completed in 6-13 days. Pupation required only a day. Total developmental time was 9-16 days with variation largely among individuals from the same egg mass rather than representing interspecific differences among different chironomids. In a *Dicortendipes* sp. egg mass, for example, the first adults emerged in 10 days, and the last in 15. There were no significant differences in rates of development from eggs collected in April, June and November. Field data for *Cricotopus* sp. suggested that developmental rates in the stream were even faster than in the laboratory (Fig. 3).

Generation times of chironomids in Sycamore Creek are as fast or faster than previous records for this family. Oliver (1971) reported that *Chironomus strenskei* of the Amazon basin has a developmental time of 10 days at 30 C. Hynes (1975) found chironomid pupae 18 days after flow resumed in a Ghana stream.

Probezzia sp. egg clusters were collected from exposed, but moist *Cladophora glomerata* mats, and were similar to those described by Thomsen (1937) in New York. Hatching required a maximum of 3 days, and larvae completed development in 9 days. Pupation required only a day. Total developmental time, 11-12 days, is much faster than the

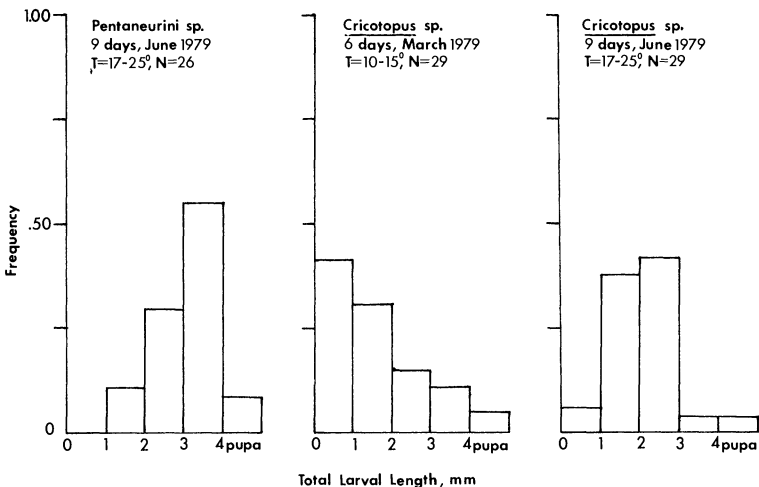


Fig. 3. — Size-class (total length in mm) distributions of chironomid species from colonization trays

2-month period required by *Probezzia glabra* and *Bezzia varicolor* (Thomsen, 1937). Sun (1974) recorded 4-week generation times for two *Culicoides* species in laboratory culture.

The life history of *Tabanus dorsifer* is considerably different from smaller dipterans just discussed. This species has the longest known generation time of any aquatic insect in Sycamore Creek (a year), plus a 6-month larval diapause (Burger, 1977). Adults emerged in spring, and reproduction occurred in July and August.

Dormancy. — Dormant stages, particularly diapause, are common in insect life cycles when favorable periods for active stages are separated by relatively predictable unfavorable periods; hence dormancy is an adaptation to temporally varying environments (Tauber and Tauber, 1976). Dormancy allows temperate lotic insects to avoid temperature extremes and to time hatching to coincide with food inputs (Cummins, 1974; Hynes, 1970). Insects in temporary aquatic habitats avoid drought by several dormancy mechanisms, including diapausing eggs, burrowing into substrates (larval diapause) and entering anhydrobiotic stages (Belk and Cole, 1975; Hinton, 1968; Hynes, 1970; Wiggins, 1973; Williams and Hynes, 1976).

A striking characteristic of most Sycamore Creek species was the absence of any dormancy in their life cycles. Rarity of dormancy is a significant difference between insects in temperate lotic and desert lotic habitats, and between insects in temporary lotic and lentic habitats. This may be due to the extreme temperature and discharge regimes of desert streams. Substrate temperatures in dry stream beds can be high; soil surface temperatures of 65 C have been recorded in the Sonoran Desert (Hadley, 1970). Only two aquatic insects (both chironomid species) can tolerate temperatures this high (*via* anhydrobiosis) (Hinton, 1968). No Sycamore Creek insects are known to possess such physiological capabilities.

Flash floods may also contribute to rarity of diapause because of substrate scour and abrasion from sediment particles. It was rare to find any eggs remaining on rocks, even large boulders, after flooding in Sycamore Creek. Channel scour in desert streams during flash floods may occur to depths greater than a meter (Leopold, 1962). Under such extreme conditions, quiescent eggs and larvae are more vulnerable to destruction than active stages (*i.e.*, aerial adults), and dormancy would not confer a selective advantage unless coupled with selection of less severe habitats. The two species in Sycamore Creek known to have a diapause stage, *Mesocapnia arizonensis* and *Tabanus dorsifer*, successfully complete that stage only where extreme conditions are absent. Stonefly egg diapause occurred in high elevation tributaries where temperatures are lower and desiccation less likely, due to persistence of moisture and continued runoff (Thomsen and Schumann, 1968). In addition, substrate scour is less common due to less frequent and less severe flooding nearer headwaters. Tabanid larvae diapause deep within the substrate (Burger, 1977), thus avoiding high surface temperatures, desiccation and scour from any but the most severe floods.

Influence of drought on life-histories. — Rapid development was a common characteristic of Sycamore Creek insects. Mayflies, small dipterans and *Graptoxcorixa serrulata* developed as fast or faster than any previously recorded. The situation parallels aquatic insects of temporary waters, such as culicid species, that complete development in 3-21 days (Matthews, 1976; McDonald *et al.*, 1973), and insects in other temporary habitats, such as animal carcasses, dung and rotting vegetation. *Musca vetustissima*, a fly that inhabits fresh dung, can complete development in 2-5 days (Matthews, 1976). Calliphorid (blowfly) larvae in carrion can complete development in a similar length of time, and 2-week developmental times have been reported for *Sarcophaga* species and *Drosophila funebris* in dung, carrion and rotting fruits (James, 1947).

Some Sycamore Creek insects, particularly beetles and caddisflies, developed at rates similar to temperate counterparts (ca. 1200 deg days). These taxa avoided drought by behavioral mechanisms, mainly habitat selection by ovipositing adults. Beetle adults oviposited either in deep pools that would retain surface water for the

length of larval development or in flowing main channel segments. Caddisfly adults, such as *Helicopsyche mexicana*, oviposited in upstream segments of cobble riffles. Many riffles represent extensions of impermeable barriers that force groundwater to the surface (Thomsen and Schumann, 1968); thus surface water may persist longer. Species with rapid development exhibited little obvious habitat selection.

Influence of floods on life histories. — Floods have a significant impact on aquatic insects in desert streams. Flood losses averaged 86% for all taxa except hemipterans (all stages) and adult beetles (Table 3), which exhibited behavioral avoidance of floods, either by flying out or swimming to protected microhabitats, such as riparian vegetation, along the channel edge. Because floods are seasonally distributed, I expected reproduction in species with high flood mortalities to occur only when probability of flooding was low. A formal comparison of reproductive periods and annual flood probability curves was, therefore, conducted (Fig. 4).

Probability of flooding was calculated from 19 years (1960-1979) of discharge data from a U.S. Geological Survey gauging station 17 km upstream from the mouth of Sycamore Creek. Dates of floods were recorded for each year. Extended high flows, common in winter, were recorded only as the initial date. For a given developmental time, probability of successful reproduction was calculated by summing the number of years in which a flood did not occur during a hypothetical developmental period and dividing by total years of record. Calculations for each day of the year were plotted as an annual curve. Separate curves were constructed for developmental times of 10, 21, 35 and 50 days (Fig. 4). For example, suppose a *Helicopsyche mexicana* female oviposited on 1 January. With a developmental time of 50 days, total developmental period would be 1 January-19 February. Floods did not occur during that period in 7 years of record; thus the probability of successful reproduction on 1 January would be 7/19 (0.37).

The method assumed that one flood did not increase the likelihood of another. This assumption is valid for summer floods, because rainfall from intense thunderstorms results in surface runoff and little absorption by soils (Burkham, 1970). Runoff from additional precipitation is thus little influenced by soil moisture levels. Winter precipitation is less intense and more is absorbed by soils, so further precipitation would likely result in greater runoff. This assumption therefore tends to overestimate probability of successful reproduction in winter because of continuous high flows that interfere with oviposition.

TABLE 3.—Losses of macroinvertebrates from flooding in Sycamore Creek (mean values from quantitative samples taken before and after nine floods, August 1977 to October 1979)

Taxon	% loss
Ephemeroptera (all taxa)	96
<i>Baetis quilleri</i>	80
<i>Leptohyphes packeri</i>	96
<i>Tricorythodes dimorphus</i>	96
Trichoptera (all taxa)	74
<i>Helicopsyche mexicana</i>	74
<i>Cheumatopsyche arizonensis</i>	68
Diptera	
Chironomidae spp.	78
Ceratopogonidae spp.	77
Coleoptera (all taxa) adults	0
larvae	89
Hemiptera	
<i>Grafcocorixa serrulata</i>	28
<i>Abedus herberti</i>	0
All taxa	86

The method also assumed that developmental times did not vary greatly during the year. Temperature is viewed as the dominant factor affecting developmental times in lotic insects (Lehmkuhl, 1979), and recent laboratory determinations of growth rates of Sycamore Creek insects indicate significant temperature effects. However, field growth rates may not vary greatly. Organisms could locate preferred thermal regimes because of the high degree of diel and microhabitat variation and generally warm temperatures of Sycamore Creek throughout the year. Some species do exhibit temperature independence. Smith (1975) reported that the length of the first instar of *Abedus herberti* was not significantly different at 18, 22 and 31 C.

For developmental times of 10 and 21 days, representative of mayflies, small dipterans and *Graptocorixa serrulata*, probability of successful reproduction was high (> 0.5) throughout the year. Although mayfly and small dipteran larvae were demonstrated to have high mortality caused by floods (Table 3), there is little influence on reproductive timing, hence no selection for seasonality. Brief developmental periods in conjunction with warm air temperatures allow continuous reproduction by these organisms with high probability of success at any time of year.

For longer developmental times, characteristic of beetles and caddisflies, the curves become bimodal with highest probability of successful reproduction during spring drought and after summer rains (Fig. 4). For nine of 10 beetle species, total reproductive periods as measured by the presence of larvae extended into low probability times, but peak abundance of larvae occurred when probabilities were high (Fig. 4).

One beetle, *Tropisternus ellipticus*, reproduced throughout spring and summer despite a low probability of success in July and August. This species apparently responds to similar reproductive cues in different parts of its extensive range, since its reproductive period in Oregon is the same (Ryker, 1975). Its success in Sycamore Creek, as measured by abundance and persistence, resulted from an initial burst of reproductive activity by overwintering adults in spring after winter flooding. The presence of many widespread Nearctic species in Sycamore Creek may be a result of similar reproductive timing.

Two groups of caddisflies may be distinguished, those that inhabit tributaries and springs (*Limnephilus* sp. and *Marilia* spp.) and those of the main channel (all other

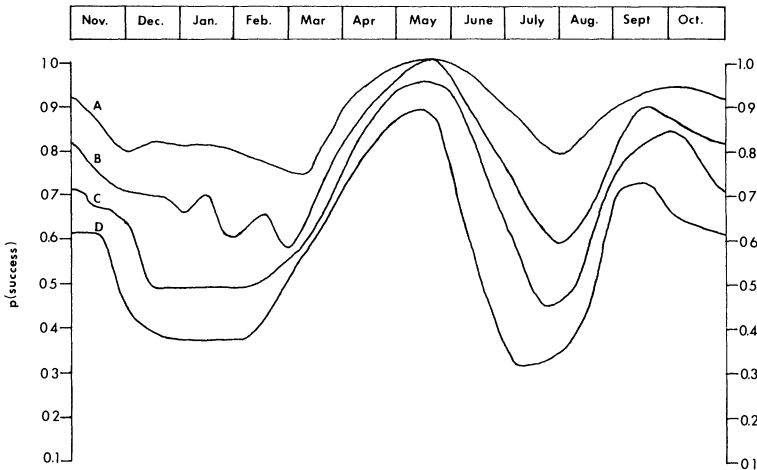


Fig. 4. — Annual flood probability curves for projected developmental times of 10, 21, 35 and 50 days based on 19 years of discharge records for Sycamore Creek; A, 10-day developmental time; B, 21 days; C, 35 days; D, 50 days. Probability of successful reproduction, p (success), equals the probability of no floods during larval development if oviposition occurred on that day. See text

species). Tributaries and springs are relatively protected habitats because of the small area of watershed contributing to runoff, and continuous reproduction would be advantageous. However, continuous reproduction by main stem species would be disadvantageous due to extended periods when the probability of successful reproduction was low (Fig. 4). From November 1978 to April 1979, a period when several large floods occurred, caddisflies were not found at any main stem site. When caddisflies recolonized in spring, they were initially at lower main stem sites and were thus probably derived from Verde River populations. Thus main stem caddisflies were successful during average precipitation regimes, but were extirpated in Sycamore Creek during extreme years.

Because floods select against dormant stages within stream sediments and cause high mortality of immatures for most taxa, aerial adults become the resistant life stage. As a consequence, community responses to floods, particularly recolonization and community recovery (especially species composition and richness), are shaped by availability of adults that left the stream prior to flooding (Gray and Fisher, 1981). Isolated floods have little impact on invertebrate communities because of a high probability that adults are nearby to recolonize rapidly. Frequent floods, however, may have long-term effects on species composition and richness through extirpation of taxa with long development and high flood mortality (*e.g.*, main channel caddisflies).

The hydrologic extremes of drought and floods are major selective pressures in desert streams. The importance of floods is related to the large, sudden increases in flow that mobilize small substrate particles and cause extensive scour and fill throughout the channel. In contrast, mesic streams rarely experience rapid, hundred-fold increases in discharge, and perennial flow creates coarse, armored substrates resistant to scour by removing finer particles (Leopold *et al.*, 1964). When large floods do occur in mesic streams, the fauna is decimated and recovery is relatively slow (Hoopes, 1974), indicating that the fauna has not evolved special adaptations for such infrequent events. Similarly, the fauna exhibits few specific adaptations for drought avoidance in streams where such events are rare (Hynes, 1958).

The evolution of particular life history traits in aquatic insects is thus dependent, at least in part, on the nature of channel processes and the predictability of major climatic events. For example, resting stages are rare in streams with rapid increases in discharge and highly mobile substrates, whereas these stages are common in other streams without such physical characteristics. Analyses similar to the flood-frequency curves presented here may assist in identifying critical "cues" regulating life histories and aid in predicting evolutionarily recent, man-made changes in stream ecosystems.

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