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# Diel Emergence, Swarming and Longevity of Selected Adult Aquatic Insects from a Sonoran Desert Stream

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**ABSTRACT:** Diel emergence patterns, swarming and mating behavior, and longevity of seven taxa of adult aquatic insects (Diptera, Ephemeroptera, Trichoptera) from Sycamore Creek, Arizona, were examined. Emergence was synchronized and generally occurred during the 1st 2 hr after dusk; however, the mayfly *Tricorythodes dimorphus* emerged 3-6 hr later. In the laboratory, adults lived for <12 hr (Tricorythidae) or >24 hr (all other taxa) at 25 C. High air temperature (38 C) reduced adult longevity by 47-78%. Mating swarms were observed only at dusk, dawn and early morning. Adult aquatic insects in Sycamore Creek possess life history traits (rapid development, synchronized nocturnal emergence, reduced daytime flight and bimodal adult longevity) that are advantageous in desert streams which periodically dry and flood and are surrounded by a hot, desiccating, riparian habitat containing numerous insectivores.

## INTRODUCTION

Most adult aquatic insects emerge from lakes or streams to mate; females then oviposit in the aquatic habitat. Successful reproduction depends, in part, on the adaptive physiological and behavioral traits that adults possess for life in the terrestrial environment. Three important traits of the adult stage are: (1) time of emergence (season or time of day); (2) location, time and behavior of swarming and mating, and (3) longevity of winged forms (subimago and imago). These characteristics influence individual reproductive success by determining physical conditions, abundance of potential mates and abundance and efficiency of predators encountered by emergent adults. Adult life span also affects the adult's potential contribution to recolonization after floods.

Assuming the environment has molded, through natural selection, life history patterns exhibited by aquatic insects, the influence of the terrestrial environment on emergent aquatic insects can be deduced by comparing life history traits of adult insects from different environments. For example, many north temperate (in early spring) and arctic aquatic insects have diurnal emergences (*e.g.*, Morgan and Waddell, 1961; Thomas, 1970; Danks and Oliver, 1972a,b; Flannagan, 1978) while tropical aquatic insects have predominately nocturnal emergences (Corbet and Tjønneland, 1955; Tjønneland, 1960; Elouard and Forge, 1978; Edmunds and Edmunds, 1980). Presumably, the detrimental effect of low nighttime air temperature on emerging adults has increased the adaptive value of daytime emergence in cold northern regions (Morgan and Waddell, 1961; Danks and Oliver, 1972a, b; Flannagan, 1978; Edmunds and Edmunds, 1980). In addition, selection pressures associated with intraspecific mating and avoidance of riparian insectivores feeding on aquatic insects (*e.g.*, Orians, 1966; Belwood and Fenton, 1976; Sjöberg and Danell, 1982; Swift *et al.*, 1985) may have contributed to adult emergence patterns and mating behaviors (Macan, 1958; Corbet, 1964; Edmunds and Edmunds, 1980; Sweeney and Vannote, 1982).

Stream corridors in the Sonoran Desert have several characteristics that are accentuated in comparison with nondesert streams elsewhere and that may influence insect life histories. In particular, the adjacent terrestrial environment has high summer air temperature and low humidity that create severe desiccating conditions. Insectivorous predators such as birds and bats are abundant (*e.g.*, Barbour and Davis, 1969; Carothers *et*

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*al.*, 1974; Stamp, 1978) and desert streams are periodically disturbed by flash flooding and drying. Although flash floods in Sonoran Desert streams often last only a few hours, aquatic insect populations are decimated. Rapid postflood recolonization of these streams results from the growth of surviving eggs and immatures, immigration from undisturbed areas, and oviposition by aerial adults (Gray and Fisher, 1981; Fisher *et al.*, 1982; Jackson, 1984). Adults that live longer than 24 hr (referred to as long-lived in this study) are more likely to be present for oviposition after flash floods than adults living less than 24 hr (short-lived), many of which die before flood waters recede.

I examined diel emergence patterns, swarming behavior, and the effect of air temperature on adult longevity for several aquatic insect taxa of Sycamore Creek, Arizona. These adult life history traits are interpreted in the context of the physical conditions in the riparian habitat, predator abundance and recolonization after flash flooding.

#### MATERIALS AND METHODS

Sycamore Creek is an intermittent Sonoran Desert stream, 32 km NE of Phoenix, Arizona. Flash floods occur, on the average, twice per year but can range up to nine times annually (usually between April and November). Flash floods normally recede to pre-flood levels in a few hours. Between summer floods, discharge is low (approximately 0.05 m<sup>3</sup>/s), mean velocity is moderate (0.15 m/sec), and the water is warm (18-27 C). By contrast, thermal conditions in the adjacent terrestrial environment can be extremely harsh compared to the aquatic habitat. Summer air temperature (2 m above ground) varies between 19 and 44 C and relative humidity is between 10 and 50% (Fig. 1). Terrestrial insectivores are numerous and feed near the stream, especially during the day (adult odonates, birds, spiders) but also at night (bats, spiders). More complete descriptions of Sycamore Creek are given in Fisher and Minckley (1978) and Fisher *et al.* (1982).

Adult life histories were examined from spring to midautumn in 1982 and 1983. The insects studied (*see* Table 1) compose 20 of the 99 insect taxa found in Sycamore Creek (Gray, 1981), yet represent 85% of total macroinvertebrate numbers and biomass and an even greater proportion of emerging insects (Gray, 1980). These insects are multivoltine and emerge throughout the year. Development time from egg to adult is between 7 and 50 days, depending on the species (Gray, 1981). Diel emergence patterns were quantified using 10 450-cm<sup>2</sup> emergence traps placed randomly in a 100-m reach of stream. Emergence traps were constructed from plastic buckets with removable net tops (0.3-mm mesh). Screens (0.3-mm mesh) on the sides of the traps allowed water to flow through the sampler, maintaining current and ambient oxygen and temperature. On two dates (5-6 July and 28-29 July, 1983), traps were examined and light intensity and temperature were recorded every 2 hr for 24 hr. On several other dates more general field observations of emergence, molting, mating behavior and adult longevity were made. Adult longevity was also determined by allowing late instar immatures to emerge under controlled conditions in laboratory environmental chambers (25 C and natural photoperiod). In the laboratory, adults were placed in jars covered with netting to permit air circulation and containing wet sponges to provide water for consumption. Time of molting from subimago (if present) to imago and time of death were recorded under these conditions. The effect of high air temperature on adult longevity was determined using laboratory environmental chambers set at 25 C and 38 C.

#### RESULTS AND DISCUSSION

*Chironomidae*.—The emergence pattern of Chironomidae (comprising 13 genera, Gray, 1980, 1981) was more varied than that of other insect groups examined here. Although emergence from the stream occurred throughout the 24-hr period except at midday, most individuals (69%) emerged between 1900 and 2100 hr (Fig. 2). Evening and morning mating swarms were present, generally over land and usually 1-10 m but up to 30 m from the stream. Mating and oviposition were not observed. High tempera-

ture (38 C) reduced adult longevity in the laboratory by approximately 50% (Table 1) and mortality, presumably due to physiological exhaustion, was observed during the heat of the day at the study site. (Some variance in emergence time and longevity may be due to grouping several species into a single taxon.)

Chironomids have been generally observed to emerge continuously throughout a 24-hr period at other sites, with maximum emergence of some species occurring at dusk and night (Morgan and Waddell, 1961; Nielsen, 1962; Oliver, 1971; Coffman, 1973; Wartinbee, 1979; Singh and Harrison, 1982; and others). Behavior patterns of adult chironomids from Sycamore Creek differed from those reported elsewhere since variance in emergence time was much smaller and daytime emergence and swarming were rare. In addition, more adults emerged per 24 hr from Sycamore Creek than from most streams. The highest single-day emergence reported in the literature is approximately 800 individuals·m<sup>-2</sup>·d<sup>-1</sup> (Wartinbee and Coffman, 1976). In Sycamore Creek, chironomid emergence averaged 666 individuals·m<sup>-2</sup>·d<sup>-1</sup> over 9 months, with a maximum of 2690 individuals·m<sup>-2</sup>·d<sup>-1</sup> in July (Jackson and Fisher, 1986).

*Tipulidae: Cryptolabis sp.* — Emergence of *Cryptolabis* sp. occurred between 1900 and 2100 hr (Fig. 2) (97-100%) and swarming occurred in the evening. No early morning or daytime mating swarms were observed in the field, although mating occurred in emergence traps and in the laboratory at all times. The Eriopterini, which includes *Cryptolabis*, has true mating swarms, but like many other tipulids, swarming is apparently not requisite to mating in this species (LeSage and Harrison, 1981; Prichard, 1983; my observations). Copulation lasted up to several minutes and oviposition behav-

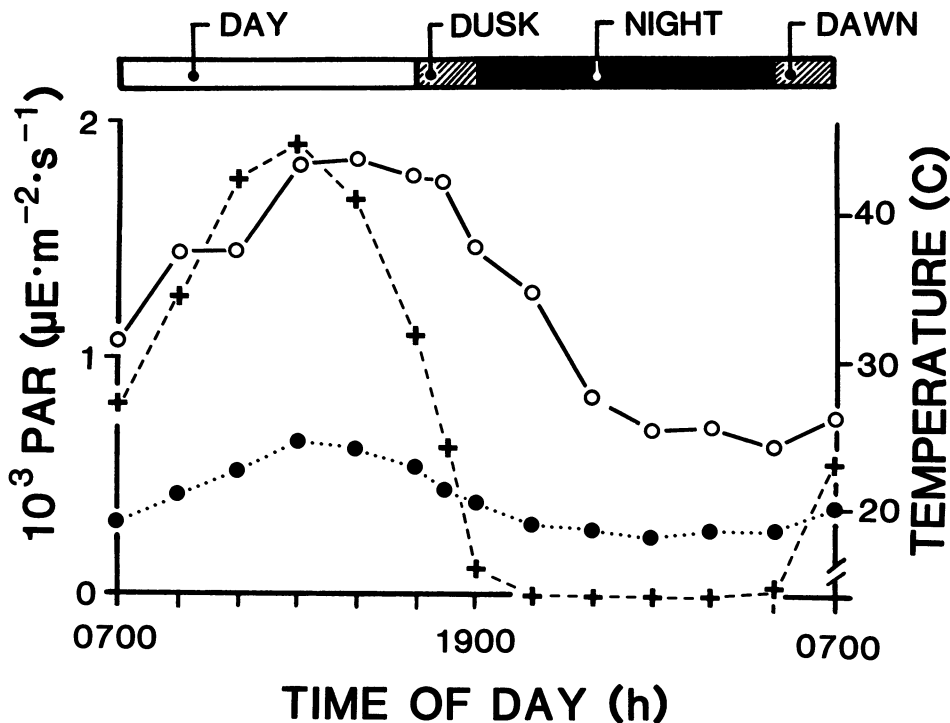


Fig. 1.—Diel changes in photosynthetically active radiation (PAR,  $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) (+), water temperature (C) (●) and air temperature (C) (○) on 5-6 July 1983 at Sycamore Creek, Arizona

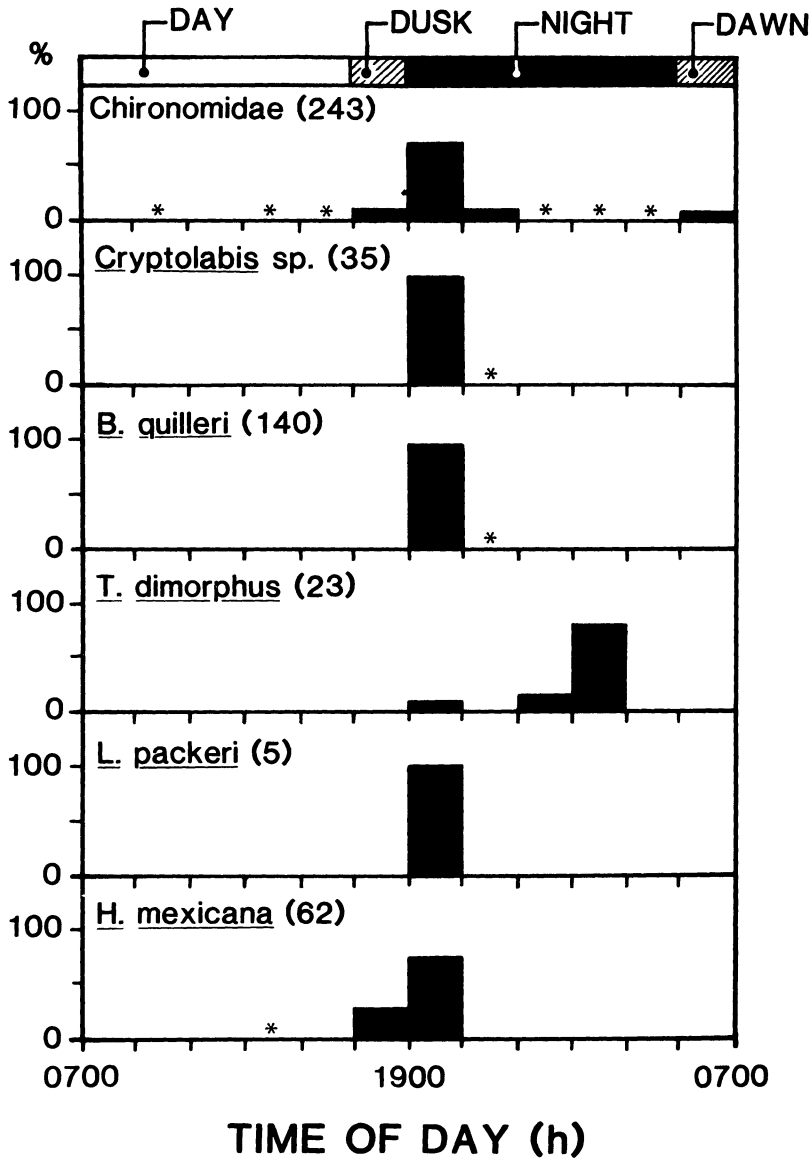


Fig. 2. —Emergence patterns of aquatic insects of Sycamore Creek (for 5-6 July and 28-29 July 1983) expressed as percent of total emerging during 2-hr periods. There was no significant difference between dates. Numbers in parentheses (n) represent total individuals captured in traps. (\*) indicates <5%

iors observed at the surface of the stream were similar to behaviors of *Cryptolabis magnistyla* Alexander reported by Hynes (1963).

*Cryptolabis* sp. appeared to imbibe water from sponges in the laboratory, especially at high temperatures. Water loss can be a problem for tipulids (Prichard, 1983) and may limit adult dispersal by keeping adults in humid areas close to the stream (e.g., LeSage and Harrison, 1981; my observations). Although the longevity of *Cryptolabis* sp. was significantly reduced by desiccating conditions, adults lived over 30 hr at 38 C (Table 1).

*Baetidae*: *Baetis quilleri* Dodds. — Most *Baetis quilleri* emerged between 1900 and 2100 hr (Fig. 2) (95-100%) and molted from subimago to imago between 2300 and 0500 hr, most often between 0200 and 0500 hr. Morning and evening mating swarms occurred both over and away from water. Swarming occasionally began before dusk in spring and autumn, when evening air temperature was lower. For other species of *Baetis*, the emergence period occurs during the daytime or evening and lasts 2-12 hr (e.g., Sprules, 1947; Elliott, 1967; Boerger and Clifford, 1975; Edmunds *et al.*, 1976; Elliott and Humpesch, 1983; Harper *et al.*, 1983).

Imagos were observed swarming at 1900 hr, indicating that adults can live 24 hr, but daytime sweeping of riparian grasses and shrubs close to the stream yielded no mayflies. Males found 30 m from the stream indicate *Baetis quilleri* adults move away from the stream after emergence, as do some temperate zone species of *Baetis* (Edmunds *et al.*, 1976; Edmunds and Edmunds, 1980).

No submergence of females for oviposition, a behavior attributed to some species of *Baetis*, was observed; females appeared to lay eggs by touching their abdomens to the water while flying (see Elliott and Humpesch, 1983, for review of *Baetis* oviposition behavior). Low light levels during these periods limited visibility and impaired observation of oviposition, but no egg masses were found on partially submerged objects as has been described for other *Baetis* species and for caddisflies (see below).

Field and laboratory observations indicated winged forms of this mayfly live for approximately 24 hr at cooler temperatures, but longevity was reduced by 73% at high temperatures (Table 1).

TABLE 1. — Longevity (time from emergence to death) of Sycamore Creek adult aquatic insects exposed to two environmental conditions (25 C and 38 C). Significance of differences tested with the Mann-Whitney U test

Taxon	Adult longevity		
	At 25 C (hours $\pm$ 1 SD)	At 38 C (hours $\pm$ 1 SD)	
Diptera			
Chironomidae*	62.5 $\pm$ 31.0 ( 50)**	32.0 $\pm$ 13.5 (79)	P < 0.002
Tipulidae: <i>Cryptolabis</i> sp.	104.2 $\pm$ 43.8 ( 22)	31.2 $\pm$ 14.0 (31)	P < 0.003
Ephemeroptera			
Baetidae: <i>Baetis quilleri</i>	22.6 $\pm$ 8.9 ( 15)	6.0 $\pm$ 0.0 ( 2)	P < 0.029
Tricorythidae: <i>Leptohyphes packeri</i>	11.3 $\pm$ 6.0 (104)	6.0 $\pm$ 0.0 ( 8)	P < 0.282
Tricorythidae: <i>Tricorythodes dimorphus</i>	8.4 $\pm$ 5.4 ( 5)	***	
Trichoptera			
Helicopsychidae: <i>Helicopsyche mexicana</i>	54.0 $\pm$ 14.7 ( 9)	12.0 $\pm$ 10.0 ( 6)	P < 0.001
Hydropsychidae: <i>Cheumatopsyche arizonensis</i>	54.0 $\pm$ 17.0 ( 6)	22.8 $\pm$ 8.2 ( 5)	P < 0.030

\*Comprised of 13 genera

\*\*Number in parentheses (n) represents individuals sampled

\*\*\*No data available

*Tricorythidae*: *Leptohyphes packeri* Allen. — *Leptohyphes packeri* emerged between 1900 and 2100 hr in summer (Fig. 2) and earlier (but still after sunset) in mid-autumn. Numbers in the emergence traps were low but field observations confirmed emergence time (Jackson, 1984). Molting to imago took place between 0300 and 0500 hr.

Mating swarms were observed between 0500 and 1000 hr over sandy runs of stream. Swarming behavior was similar to that described for *Tricorythodes dimorphus* (see below), but no females were found in swarms of *Leptohyphes packeri*. Mating and oviposition were not observed.

No imagos were found in the field during afternoon and evening, implying that adults did not live 24 hr. This was confirmed with laboratory observations where emergents lived for approximately 11 hr (Table 1). Although some adults in the laboratory were still alive 13 hr after emergence, none was capable of flight. No other published descriptions of adult behaviors in *Leptohyphes* are available but the adult life history traits of *Leptohyphes packeri* in Sycamore Creek are typical of tricorythids (see below) and many tropical mayfly species (Tjønneland, 1960; Elouard and Forge, 1978; Edmunds and Edmunds, 1980).

*Tricorythidae*: *Tricorythodes dimorphus* Allen. — *Tricorythodes dimorphus* emerged later than most species, with 93 to 100% found in emergence traps or on partially submerged rocks between 2400 and 0300 hr. A few individuals emerged earlier (1900-2100 hr). Subimagos molted to imagos between 0300 and 0530 hr, especially at dawn (0430 to 0530 hr). Swarming occurred in the morning, over pools and occasionally over faster water. Swarms were created by adults flying downstream in a sinusoidal fashion for 3-6 m, then flying quickly upstream to repeat the pattern.

This pattern has been observed for other species of *Tricorythodes* (Hall *et al.*, 1975; Edmunds *et al.*, 1976). As reported in previous studies of *Tricorythodes*, males and females were present in the swarm. Mating and oviposition were not observed. The few adults that successfully emerged in the laboratory lived less than 12 hr (Table 1). In the field, no winged forms were ever found in the afternoon and only subimagos were captured during the evening.

*Tricorythodes atratus* McDunnough has been studied in Minnesota (Hall *et al.*, 1975). It has an adult life history similar to that of *Tricorythodes dimorphus*, although emergence is less synchronized. Tropical tricorythids generally exhibit synchronized nocturnal emergence and short adult longevity (Tjønneland, 1960; Elouard and Forge, 1978; Edmunds and Edmunds, 1980).

*Helicopsycheidae*: *Helicopsyche mexicana* Banks. — *Helicopsyche mexicana* emerged earlier (1800-2100 hr, 90 to 100%) than other insects in Sycamore Creek (Fig. 2). Some adults appeared in the emergence traps during the afternoon but I attribute this to pupal disturbance from setting and monitoring emergence traps. No mating swarms were located but I observed individual adult flight that was erratic and covered short distances at dawn and dusk in streamside vegetation. Mating was observed in emergence traps at 2100 hr, indicating that adults can mate immediately after emergence and swarming is not required. Rather than swarming, mates may be attracted with sex pheromones, as was recently demonstrated for *Helicopsyche borealis* (Hagen) (Resh *et al.*, 1984).

Trichoptera emerge and mate in a manner similar to other aquatic insects but their oviposition and postoviposition behaviors can be unusual. Some female Trichoptera oviposit under water (Ross, 1944), leave the water after oviposition, and die on land (Denning, 1937; Badcock, 1953; Corbet, 1966; Tozer *et al.*, 1981). Underwater oviposition for *Helicopsyche mexicana* in Sycamore Creek was confirmed by egg masses attached to partially submerged objects. Reemergence was not observed in this study. Longevity of *H. mexicana* was reduced significantly by high temperature. Adults lived more than 2 days at 25 C but only 0.5 day at 38 C (Table 1).

*Hydropsychidae*: *Cheumatopsyche arizonensis* (Ling). — Only seven adult *Cheumatopsyche arizonensis* emerged in traps (1900 to 2100 hr). Flight behavior was similar to that described for *Helicopsyche mexicana*. Neither mating nor oviposition were observed. High

temperature affected *C. arizonensis* less than *Helicopsyche mexicana* (Table 1).

*Adult life history traits and the terrestrial environment.*—It has been hypothesized that patterns of adult aquatic insect emergence and mating evolved in response to climatic conditions and predation pressure in the terrestrial environment (Morgan and Waddell, 1961; Edmunds and Edmunds, 1980). The general applicability of this hypothesis remains to be demonstrated because almost all studies have been conducted at north temperate sites. Aquatic insects of north temperate regions are noted for both crepuscular and daytime emergence and swarming periods. Emergence periods can often last for several hours (e.g., Corbet, 1966; Hall *et al.*, 1975; Harper *et al.*, 1983; Singh and Harrison, 1982). Several emergence and swarming patterns are usually found in a single north temperate community (e.g., Morgan and Waddell, 1961; Wartenbee, 1979). In contrast, adult insects of Sycamore Creek showed little variation in adult behavior (Fig. 2). Nocturnal emergence periods were short and were followed by mating, oviposition and death within 12 hr or, in long-lived taxa, reduced daytime activity. Thus, adults did not fly during the hottest period of the day and flying adults were exposed only briefly to daytime and nighttime predators in the terrestrial ecosystem. That synchronized nighttime emergence and reduced daytime flight occur in all Sycamore Creek insect taxa, many of which are only distantly related, is evidence that these life history characteristics are advantageous in desert stream corridors.

*Postflood recolonization.*—Change between pre- and postflood stream community structure (species composition, richness and evenness) depends in part on each species' recolonization rate. Postflood recolonization rates are influenced by the severity of disturbance (duration and magnitude) and life history traits. Flash floods in desert streams generally last for a few hours. Adults of all species studied, except tricorythid mayflies, lived more than 24 hr in the laboratory (at 25 C) and were found throughout the day in the riparian vegetation surrounding the stream. Thus, aerial adults for stream recolonization are always present during cool periods of the year. This confirms the predictions of Gray and Fisher (1981) who attributed most recolonization of Sycamore Creek to aerial adults. Some taxa must depend heavily on egg survival or drift for recolonization because adult longevity is short (e.g., tricorythids) or adult mortality is extremely high during hot weather (e.g., *Baetis quilleri* and *Helicopsyche mexicana*). If high air temperature changes the emergent adult community surrounding the stream, then stream insect recolonization patterns after flash floods in July may differ from those after October floods. Aquatic insects with life history traits favoring rapid recolonization (a large population of aerial adults and high flood survival rates for immatures and pupae) have distinct advantages over other recolonizers. *Cryptolabis* sp. possesses both of these rapid recolonization traits (Gray and Fisher, 1981; Jackson, 1984) and often dominates postflood benthic communities (Fisher *et al.*, 1982; Jackson and Fisher, 1986). Patterns of succession at Sycamore Creek are thus a result of interaction between the stochastic environment and life history traits of individuals in the predisturbance community, a model also applied to temperate forest succession by Drury and Nisbet (1973).

In summary, insects of Sycamore Creek possess critical life history characteristics of rapid development (Gray, 1981), highly synchronized nighttime emergence, and bimodal adult longevity (<12 hr or >24 hr) which was significantly reduced by high air temperature. Swarms were found generally at dusk, dawn and early morning. These traits are advantageous in a desert stream prone to unpredictable flash floods and irregular periods of drying, and imbedded in a hot, dry riparian corridor with abundant predators.

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