The Life History of *Isonychia sicca* (Ephemeroptera:Oligoneuriidae) in an Intermittent Stream in North Central Texas[1,2]

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ABSTRACT

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The life history of *Isonychia sicca* (Walsh) was determined from samples collected in intermittent Clear Creek, Oct. 1976–June 1978, Denton Co., TX. Fall hatching nymphs formed a small overwintering brood, grew slowly through the winter and emerged in late Apr. A spring brood hatched in Mar. and emerged late May–early June. Adults from overwintering and spring broods supplied eggs which formed a 2nd generation that emerged late June–early July. Emergence began ca. 20 min after sunset and continued for ca. 2 h. The emergence period was continuous, Apr.–July 1977, with both broods and generations overlapping considerably. Average subimaginal fecundity decreased through the emergence period from 4440 to 621 eggs/female, and was positively correlated with abdominal volume. A decrease in body size was noticeable for nymphs, subimagos and imagos. The sex ratio differed for each stage: $1\male:1.6\female$, nymphs; $1.4\male:1\female$, subimagos; and, $1\male:3.4\female$, imagos. Nymphs filter particulate matter from water using long foreleg hairs as a seine. *Isonychia sicca* appears to diapause in the egg stage through dry periods. Upon fall rehydration, eggs slowly break diapause differentially through the fall with those breaking early producing the overwintering brood. Eggs breaking diapause in late fall and winter experience cool water temperatures which probably induce quiescence. Hatching begins again in spring. In a permanent stream, eggs continue to hatch through summer and fall until cool winter temperatures probably induce quiescence and resume hatching in spring.

Isonychia sicca (Walsh) is a common mayfly in north Texas streams, yet very little is known of its biology. It is a component in stream drift (Cloud and Stewart 1974); the diet of hellgrammite larvae, *Corydalus cornutus* L. (Stewart et al. 1973); and is vertically distributed in the substratum (Poole and Stewart 1976).

Comparatively little is known of the life cycles and biology of other *Isonychia* species, although the genus is common in lotic systems of North America. Brodsky (1973) discussed swarming behavior of the genus. Needham (1905), Morgan (1911, 1913), Harper and Magnin (1971) and Leonard and Leonard (1962) provided brief biological notes on *I. bicolor* (Walker), and Ide (1935a) described the egg and 1st 2 instars. Cooke (1942) published brief notes on mating behavior and the effect of temperature on the emergence of *I. christina* Traver. The classic mayfly works of Needham et al. (1935), Berner (1950, 1959), Burks (1953) and Edmunds et al. (1976) mainly provided information at the generic level. The studies of Clemens (1917) and Sweeney (1976, 1978) on *I. bicolor* and Smith (1978) on *I. fattigi* Traver represent the only major biological studies on the genus *Isonychia*.

The abundance and apparent success of *I. sicca* in an intermittent stream suggested to us that this species had possibly undergone some adaptation of life cycle to enable survival during hot, dry summer conditions. Our major objective was to determine the life cycle of *I. sicca*, giving particular attention to its adaptive strategies in an intermittent stream of north central Texas.

Three subspecies of *I. sicca* (*campestris* McDunnough, *manca* Eaton, *sicca* (Walsh)) are recognizable based on coloration of body parts, minor genitalic differences and male foretarsi:tibiae ratios (McDunnough 1931). However, reared and collected specimens used in this study were so variable in color and genitalia that some individuals could be assigned to either *I. sicca sicca* or *I. sicca manca* according to McDunnough's (1931) descriptions and key (W. L. Peters, pers. comm.). As a complete series of each subspecies from wide geographic areas was not available for further taxonomic analysis, we are referring to the species, herein studied, as *I. sicca* (Walsh) and are depositing a series of voucher specimens of all life stages at Florida A&M University, North Texas State University and University of Utah.

McCafferty and Edmund's (1979) familial classification is followed.

Study Sites

The primary Clear Creek sampling site was a series of riffles 1 km S of Bolivar, Denton Co., TX, near the F.M. 2450 bridge. A riffle ca. 18 km downstream near the F.M. 2164 bridge, 5 km N of Denton, was sampled occasionally. Substrate in riffle areas consisted of shallow limestone rubble, underlain with packed sand. The stream flowed at low to moderate levels Sept. 1976–July 1977, and Jan.–June 1978, except for a severe spate in Mar. 1977. During dry conditions, July–Sept. 1976 and July 1977–Jan. 1978, only a few scattered pools remained. A short period of flow during the 1977 dry period occurred after a 6 cm rainfall in Aug.

A remote bulb temperature recorder was installed in the stream at the Bolivar site. Due to vandalism in Dec. 1976, the recorder was replaced the following month with a submersible, continuously recording thermo-

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graph. Water temperature was also measured on each sampling date with a hand held thermometer.

Average weekly water temperatures in Clear Creek are plotted in Fig. 1. During this study dissolved oxygen (YSI Model 54 oxygen meter) ranged from 6.9–8.4 ppm, specific conductance (YSI Model 31 conductivity bridge) corrected to 25°C ranged from 680–4770 μmhos, and total alkalinity and hardness (both $CaCO_3$, APHA 1976) ranged from 127–270 ppm and 264–334 ppm, respectively. The pH ranged 8.0–8.3 (Corning digital 109 or Fisher Accumet® Model 210 pH meter).

Riparian vegetation consisted mostly of sycamore (*Platanus occidentalis* L.) ash (*Fraxinus* sp.), eastern cottonwood (*Populus deltoides* Marsh.) and hackberry (*Celtis* sp.).

During Sept. 1977 a riffle population of *I. sicca* was found in the Elm Fork of the Trinity River, 1 km E of Burger Road on McKinney Bridge Road, Denton Co., TX, ca. 13 km above its confluence with Clear Creek. Elm Fork is a permanent stream, and it flowed continuously during the Oct. 1976–June 1978 Clear Creek study period. Riparian vegetation and riffle substrate were similar to those at Clear Creek.

Materials and Methods

Eggs for rearing and photographing were collected from egg sacs of imagos attracted to light during the summer 1977 flight period. Eggs were reared in distilled water at room temperature (23°C) or in an environmental chamber under simulated stream temperature and photoperiod. Distilled water was changed every 1–2 wk. Eggs for photographing were stored in 80% isopropanol.

To determine if *I. sicca* eggs could withstand dehydration, some egg sacs were collected from imagos during the summer 1977 flight period, dried and stored in an air-tight vial. Eggs were rehydrated with distilled water in Apr. 1978 and incubated at room temperature or stream conditions.

Methods described by Towns and Peters (1978) were used to prepare eggs for scanning electron microscopy. Eggs in distilled water were measured with an ocular micrometer.

Nymphal sampling began in Clear Creek after the summer 1976 dry period. Samples were taken monthly, Oct. 1976–July 1977. On each date 4 qualitative samples were collected with a net with 363 μm mesh opening with an attached plankton bucket with 363 μm mesh opening.

In addition, cumulative qualitative samples were taken each month in Clear Creek with a 2-stage net having 1 mm and 153 μm mesh openings in the 1st and 2nd stages, respectively. A 363 μm mesh plankton bucket was attached to the 2nd stage. This net design increased chances of collecting small instars.

Isonychia sicca recruitment in Clear Creek, after the 6 mo dry period of 1977, was monitored by biweekly 2-stage net samples, Jan.–June 1978. Two-stage samples were taken monthly in Elm Fork, Sept. 1977–Apr. 1978, and biweekly the following May and June.

Twice during dry periods in the stream, 19 July and 11 Oct. 1977, substrate was removed with a post hole digger to determine water table level and collect vertical
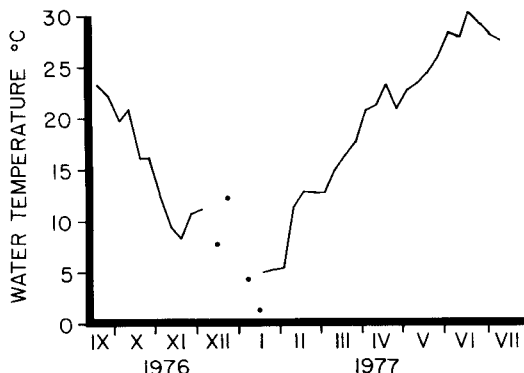

FIG. 1.—Stream temperature of Clear Creek, Sept. 1976–July 1977. Solid line = avg. weekly temperature from recording thermograph; dots = daytime readings on sampling dates.

layers of substrate for subsequent elutriation (Stewart 1975) and sucrose flotation (Anderson 1959). During dry periods existing pools were sampled with a 1 mm mesh opening kick net, and the substrate was examined under a stereomicroscope for the presence of eggs or small nymphs.

Live nymphs were reared in aquaria containing natural substrate and aerated stream water in the laboratory. Nymphal feeding was observed in these aquaria and in the stream. Newly hatched nymphs from incubated eggs were reared individually in 20 ml vials of stream water, at simulated stream temperature and photoperiod in an environmental chamber. Behavioral examinations were conducted under a stereomicroscope.

Live nymphs for gut examination were either transported to the laboratory on ice and frozen or killed in 80% isopropanol at the site and later preserved in 10% formalin. Fore- and midguts were dissected, placed in distilled water on a slide and scanned under a compound microscope at 100X.

Nymphal head capsules were measured at their greatest width with an ocular micrometer.

Subimaginal emergence and imaginal flight period were monitored during spring and summer, 1977, using two 91 cm, 30 watt fluorescent bulbs (1 white and 1 "black light") powered by a portable generator. The light trap was operated weekly during the entire emergence period from 0.5 h before sunset to 2 h after. Mayflies attracted to both lights were collected every 0.5 h and preserved in 80% isopropanol. During peak emergence, 6 June 1977, the lights were operated continuously throughout the night until sunrise the following morning. A light meter measured light intensity during sunset.

Emergences were observed in both the field and laboratory, and subimaginal box cages (Edmunds et al. 1976) were used to observe subimaginal molts. Longevity (emergence to imago death interval) was determined in the box cages at room temperature in the laboratory.

Fecundity (no. eggs in oviducts) was determined from light-attracted subimagos, since light-attracted imagos

were usually devoid of eggs. To examine potential correlation between subimaginal fecundity and body size throughout emergence, female abdomens were assumed to be cylindrical, and relative volumes calculated as $v = \pi r^2 l$, where $r = 0.5 \times$ width ab_5 and $l =$ length of $ab_2 - ab_8$, inclusive.

Results

Eggs

Isonychia sicca eggs (Fig. 2, 3) are spherical and average 242 μm in diam. Knob-terminated coiled threads (KCTs) (Koss and Edmunds 1974) are densely packed on 1 hemisphere and scattered on the other (Fig. 2–5). Chorionic tagenoform micropyles (Fig. 6) were found only on the hemisphere with few KCTs. These eggs fit the generic description of Koss and Edmunds (1974). Eggs collected from imagos over the period 1 June–1 July 1977 exhibited no size or structural change. Eggs dissected from preserved subimagos and imagos were distorted and could not be accurately measured.

Eggs from light-attracted imagos began hatching after 11 d at simulated stream ($\bar{x}$ temperature for 11 d = 29.1°C) and room conditions and continued for 11 and 17 d, respectively. No further hatch occurred until after 70 d of incubation, when 2 eggs hatched at room temperature. The total number of eggs reared was not determined.

Egg sacs that had been shelf-dried in vials for 282 d slowly disintegrated as the eggs swelled to normal size and appearance when placed in distilled water. No apparent development or hatch occurred during the 2.5 mo of incubation.

Nymphs

At 23°C the 1st stadium of 42 laboratory-hatched nymphs lasted 2 d. Twenty of these nymphs survived the 2nd stadium which averaged 4.2 d (ranged 3–5). Third instars died 1–3 d after the 2nd molt. First and 2nd instars closely fit the description of *I. bicolor* (Ide 1935a), having no evident gills and 3 differentiated antennal segments. Attempts to rear small and mid-size, field-collected nymphs to maturity in the laboratory were unsuccessful.

Forceps were 1st observed on male nymphs with head capsule width (hcw) of 0.90 mm; nymphs with hcw 0.90 mm or larger without forceps were considered female. Nymphal sex ratio of pooled samples over 0.90 mm hcw was 1♂:1.6♀ (713:1139).

Second stage nymphs fed by lowering their heads to graze on detritus in the rearing dish. These nymphs also fed on detritus accumulated on the tarsal claws from their movements in the rearing dish, bending the legs at the tibio-femoral joint to bring the claws close to the mouthparts, and cleaning 1 claw at a time.

Forelegs of middle and late instars are equipped with 2 rows of long hairs on the inner margin of the femora, tibiae and tarsi. Two rows of shorter hairs occur between the rows of longer hair on the fore tibiae. Feeding nymphs observed in aquaria and field, faced the current with outspread front legs. The current separated the hair rows, forming a v-shaped seine which filtered particulate matter from the water. Wallace and O'Hop (1979)

discussed and illustrated the coupling mechanism by which this seine is formed in *Isonychia*. Filtered particles were transferred to the hairy mouthparts by rhythmically bending each leg at the tibio-femoral joint. This action allowed the current to collapse the hair fringe, forcing filtered particles into the hairy mouthparts, where they were entrapped and then collected by the palpi. Legs were always flexed alternately.

Qualitative examination of 10 nymphal fore- and midguts, collected in Elm Fork during late fall and early winter, 1977, indicated that *I. sicca* was predominantly a detritivore, occasionally ingesting algal cells and diatoms. Two arthropod legs and a head capsule were found in 1 gut and a microcrustacean exoskeleton in another, indicating possible carnivory. One of 2 guts of final instars from Elm Fork, Oct. 1977, was completely empty; only the posterior half of the other was full. Final instars were never observed feeding in the laboratory or field. Clear Creek nymphs, frozen for gut analysis, were so damaged after thawing that guts could not be successfully extracted for analysis.

A frequency histogram was constructed from the hcw of the 4469 Clear Creek nymphs collected during 1976–77 to estimate number of instars. No well-defined, instar separations were evident, and there was a considerable amount of overlap. Measurement of 13 first, 16 second and 6 third instars (all laboratory reared) substantiated this overlap. A frequency histogram constructed for only the overwintering nymphs also produced no reasonable separation.

The average final instar hcw of Apr. nymphs was larger (2.08 mm ♂, 2.24 mm ♀) than that of July nymphs (1.74 mm ♂, 1.83 mm ♀). This decrease was nearly linear through the emergence period with females always larger than males.

Seasonal growth and size distribution of nymphs are shown in Fig. 7. A small population of nymphs was initially found in Oct. 1976, within 1 mo of rehydration; they grew through the winter and began emerging in late Apr. (Fig. 7, solid line). Limited recruitment continued Oct.–late Nov. All of these nymphs will hereafter be referred to as Generation I, overwintering brood (GI-ow). The Dec. population exhibited the greatest size range, including 3 nymphs (1♂,2♀) with black wing pads (i.e., mature nymphs). Dec. water temperatures in Clear Creek ranged ca. 8–12°C (air temperature −9 to 22°C) after the appearance of these mature nymphs. No mature nymphs were found the following Jan.–Mar.

Recruitment recurred mid-Mar. 1977, with nymphs growing quickly and emerging late May–early June (Fig. 7, dashed line). These are hereafter referred to as Generation I, spring brood (GI-s). The dotted line in Fig. 7 represents the short summer Generation II (GII). Eggs from GI-ow and GI-s adults began hatching soon after oviposition resulting in a substantial recruitment from May until the stream ceased flowing in mid-July.

Vertical substrate samples taken in mid-July 1977 at Clear Creek, during the dry period, produced no nymphs. The water table at this time was ca. 33 cm below the surface. A 6 cm rainfall 1 Aug. 1977 rehydrated the stream. First instars were found the following day, along with a few slightly larger nymphs. The stream dried again within 1 wk, and did not run again until Jan. 1978,
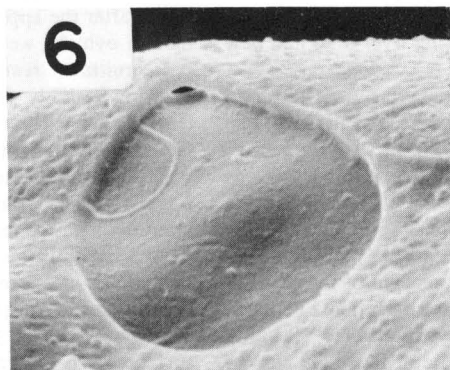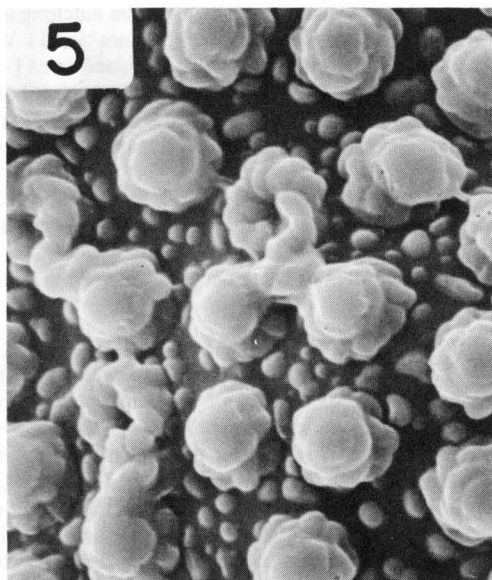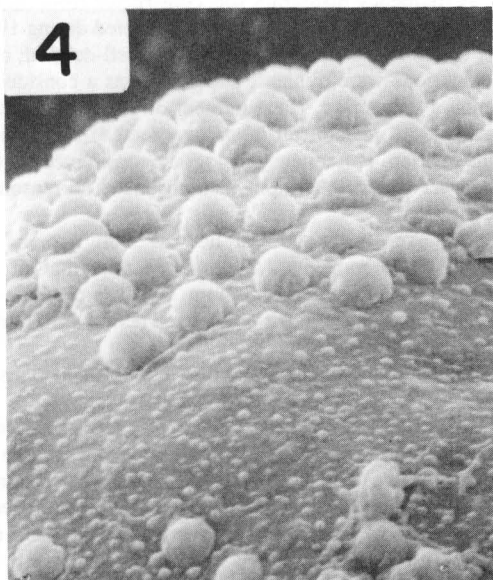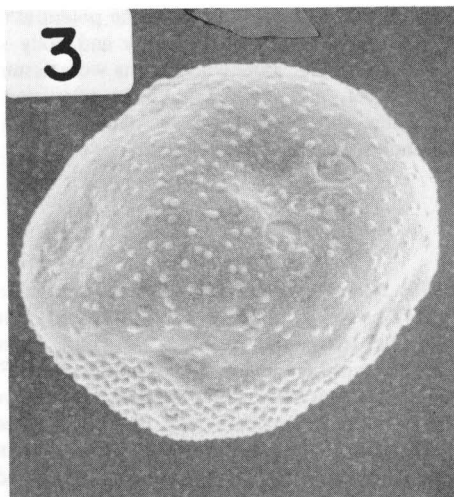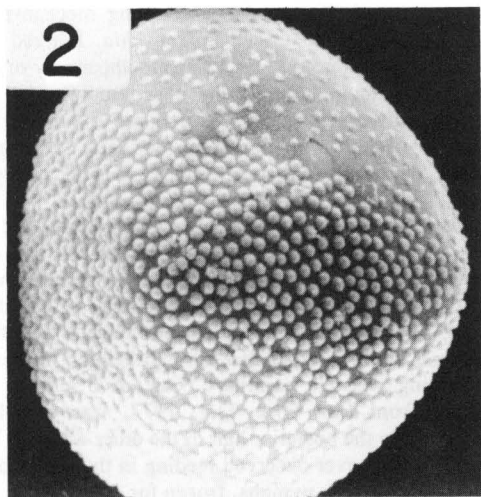
FIG. 2–6.—Scanning electron micrographs of *I. sicca* eggs. 2. Whole egg, 400X. 3. Whole egg, 300X. 4. Interface between two hemispheres, 1000X. 5. Knob-terminated coiled threads, 3000X. 6. Chorionic tagenoform micropyle, 3000X.

due to semidrought conditions. Rehydration would usually have occurred after Sept. rains. Sampling of surface substrate, vertical substrate levels and existing pools yielded no *I. sicca* nymphs during the 1977 dry period. Water table level in mid-Oct. had dropped to ca. 76 cm below the surface. However, sandy areas remained damp beneath surface rubble during the dry period.

Clear Creek rehydrated 11 Jan. 1978, after a 3 cm rainfall, but nymphs were not found until late Mar. Recruitment occurred continually from Mar. through mid-June. Emergence began in late May, when 1 final instar exuvium was found, and continued through mid-June, as indicated by the presence of mature nymphs. This growth pattern closely resembled that of the 1977 GI-s brood. Clear Creek was dry again by July 1978.

A light trap was run post-sunset on Elm Fork in mid-Sept., and 10♂'s (6 subimagos, 4 imagos) and 6♀ subimagos were collected. Emergence continued through Oct., as indicated by mature nymphs, with recruitment occurring Sept.–Oct. However, populations appeared to synchronize near the 2.20 mm hcw in Nov. (only a few larger nymphs found) and Dec. (no larger nymphs found). Recruitment did not occur in Dec. The heavy rains that rehydrated Clear Creek prevented sampling in Jan. 1978, and only 3 nymphs were collected in Feb. at the synchronized size. No nymphs were found in Mar., even though previous sampling in Mar. 1977 had produced nymphs larger than the synchronized size, suggesting a GI-ow brood similar to that of 1976–77 at Clear Creek (Fig. 7, solid line). Nymphs 1st appeared in mid-Apr. 1978, and mature nymphs were 1st found in mid-June. This Elm Fork brood was 2 wk later than the 1977 and 1978 GI-s broods at Clear Creek. Continued recruitment followed from mid-Apr. through mid-June. Emergence began in mid-June when sampling ceased, and continued thereafter, as indicated by mature nymphs.

Subimagos

Mature nymphs appeared near the surface on emergent objects near sunset and typically emerged with only their head protruding from the water. The entire molting process was completed in ca. 20 sec. Emergence began ca. 20 min after sunset, and continued for ca. 2 h, with peak emergence during the 1st h. Emergence was not observed at any other time of day. Subimagos took flight immediately after molting and were strongly attracted to light.

Emergence occurred 23 Apr.–11 July 1977, peaking on 6 June (Fig. 8), when 2023 subimagos were attracted to the light trap. Both males and females were highly attracted to the light trap, with males always outnumbering females: 1.4♂:1♀ (5551:3909).

The average size of subimagos and imagos decreased through the emergence period, as indicated by hind femoral length (Fig. 9), females being consistently larger than males.

Average subimaginal fecundity decreased almost linearly through the flight period, from 4440 to 621 eggs/female (range 4918–302 eggs), 30 Apr. and 11 July 1977, respectively. Fecundity was positively correlated with estimated abdominal volume ($r^2 = 0.94$, $\alpha = 0.05$). Estimated volume of dissected subimagos decreased by 85% and fecundity by 86% over the emergence period.

Average and range of subimaginal life span in the laboratory for both sexes were 25 and 23–29 h, respectively.

Imagos

Subimagos became more active just prior to the proximate molt. Molting time for 2 males and 2 females, from point of restlessness to complete ecdysis, averaged 10.7 min. Duration of molt from time of mesothoracic split averaged 4.5 min. Molting times were similar for both sexes.
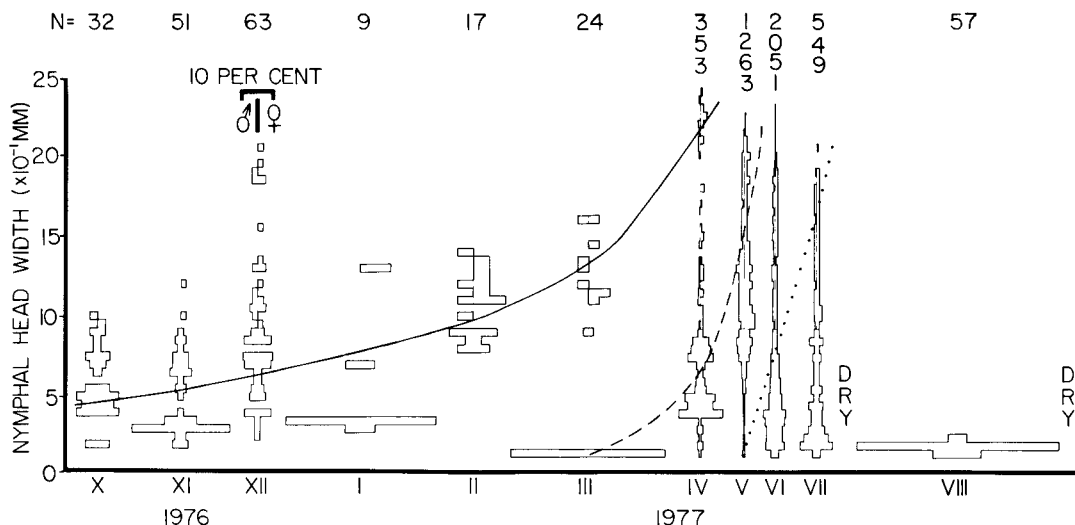

Fig. 7.—Seasonal size distribution of 4469 *I. sicca* nymphs, Oct. 1976–Aug. 1977, Clear Creek. Sexes separated above 0.90 mm size class for each month by vertical line (males left, females right). Solid curved line = proposed Generation I, overwintering brood; dashed line = proposed Generation I, spring brood; dotted line = proposed Generation II.

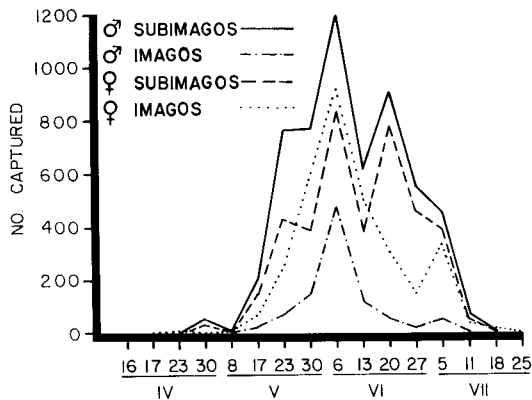ANNALS OF THE ENTOMOLOGICAL SOCIETY OF AMERICA

FIG. 8.—Number of *I. sicca* collected at light trap, Clear Creek, 1977.

The imaginal flight period occurred 23 Apr.–25 July 1977, peaking on 6 June (Fig. 8). Imaginal attraction to the light trap began ca. 20 min after sunset, generally when the light meter reading was less than 10.8 lux, and continued for ca. 1 h. Female imagos were the 1st arrivals at the light trap 88% of the time. Peak imaginal attraction occurred ca. 30 min after sunset. Imaginal activity was not observed at any other time of day. Sex ratio of light-attracted imagos was 1 ♂:3.4 ♀ (952:3208).

Mating and oviposition were not observed, even though a 24 h monitoring station was set up during peak emergence and the light trap was operated continuously throughout the night.

A few female imagos attracted to light had small egg sacs which were hemispherical in shape, and ca. 1.0 mm diam. A few larger, cylindrical egg sacs measured ca. 3.5 mm long × 1.0 mm diam. Fresh, moist egg sacs were light yellow, and immediately disintegrated when placed in water. Older, dried egg sacs were darker yellow, and were slower to disintegrate in water. The oviducts of 2 imagos with small egg sacs were full of eggs, which may indicate multiple extrusions. Nematodes were occasionally found coiled in the oviducts among the eggs of dissected females.

One female and 2 male imagos were found during the day resting underneath sycamore leaves. This was the only imaginal resting site found. At room temperature 25 males lived an average of 3.4 d in the laboratory (SD = 1.22, range 2–5 d) and 30 females 4.4 d (SD = 1.64, range 1–9 d).

Discussion

Eggs

Hatching times of fertilized *I. sicca* eggs compared favorably with those of *I. bicolor*. Clemens (1917) found that *I. bicolor* eggs initiated hatching after 14 d at 22.5–25°C and Sweeney (1978) noted 1st hatch of *I. bicolor* after 25 d at stream temperature (x̄ temp. = 17.0°C). Two eggs hatched after 70 d incubation. Sweeney (1978) found ca. 80% *I. bicolor* eggs from a single female in a given temperature regime would hatch within a week of the 1st eclosion while the remaining eggs would hatch after 4–5 wk. He postulated that variation in hatch times may be due to differences in egg

size, nutrient supply and genetic composition. Extended hatching also occurred in the field as recruitment occurred Oct. and Nov., ceased during winter and resumed Mar. (Fig. 7). This type of hatch, with low numbers recruited in fall, little or none in winter and the main hatch in spring, also occurred in *Ephemerella ignita* (Poda) (Elliott 1978) and *Heptagenia diabasia* Burks (Flowers and Hilsenhoff 1978). Elliott (1978) attributed such a hatching pattern to temperature, with extreme temperatures inhibiting hatching while moderate temperatures stimulated hatching.

Dehydrated eggs did not exhibit any development although they resumed normal appearance after rehydration. Britt (1962) showed some *Ephoron album* (Say) eggs, dried for up to 4 d would hatch after rehydration and the proper temperature cue. Edmunds et al. (1956) dried eggs of *E. album* for 2 wk but none hatched during a 6 mo incubation after rehydration.

Nymphs

Observations on the feeding behavior of *I. sicca* indicate a probable shift from predominantly grazing in the early instars to filter feeding in later instars. However, filter feeding does not appear to totally replace grazing as 1 late instar nymph was observed grazing on a layer of algae in an aquarium.

Isonychia sicca is primarily an omnivore ingesting mostly detritus and occasionally algae, diatoms and small arthropods. Similar food habits were reported for *I. bicolor* (Needham 1905, Morgan 1913, Clemens 1917), *I. fattigi* (Smith 1978) and unidentified *Isonychia* nymphs (Shapas and Hilsenhoff 1976). Coffman et al.
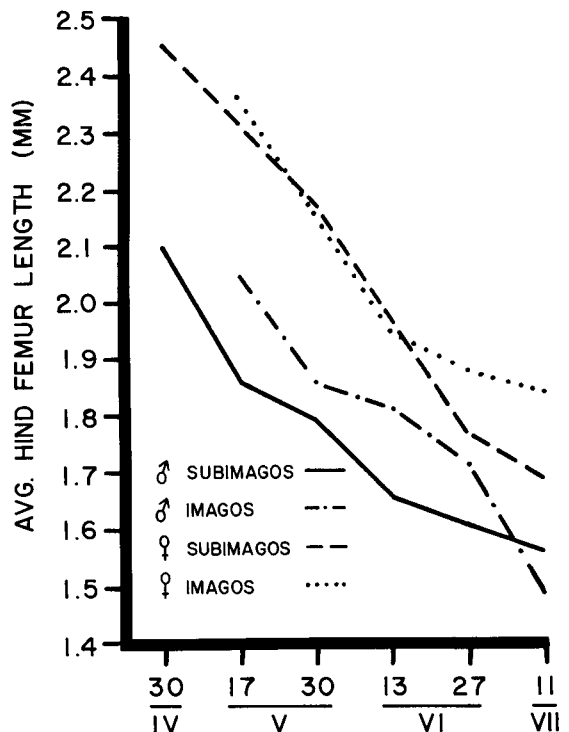

FIG. 9.—Average hind femoral length of *I. sicca* subimagos and imagos during the 1977 flight period, Clear Creek.

(1971) found ca. 60% of the caloric ingestion of *I. bicolor* to be animal, 25% algae and 15% detritus. *Isonychia sicca* is probably a passive feeder, ingesting whatever is collected during filter feeding. Carnivory by *Isonychia* nymphs may be due to ingestion of drifting exuviae or animals collected during filter feeding and not from active selection, a view also held by Clemens (1917).

A potential emergence was suggested by the presence of mature nymphs in Clear Creek during Dec. 1976. Sweeney (1976), though, found that only 5% of mature *I. bicolor* nymphs exposed to a 10–12°C thermal regime successfully emerged; none emerged at the 8–10°C regime. Clear Creek water temperature at this time ranged ca. 8–12°C. Sweeney (1976) also found that mature nymphs collected in Dec., and reared at ambient stream temperatures experienced a high winter mortality (>70%), with death occurring during ecdysis. Of the 63 nymphs collected in Dec., only 3 were mature. Thus, the lethal effects of low temperature on mature nymphs and the small number of nymphs present in the stream led us to believe the 1st significant *I. sicca* emergence did not occur until Apr.

Since no significant emergence occurred between the 1976 dry period and late Apr. 1977, fall and spring nymphs hatched from eggs deposited prior to the 1976 summer dry period and thus were broods of 1 generation (GI-ow and GI-s, respectively). Duration of the egg stage in the stream, then, ranged from ca. 2 to 9 mo. These broods hatched ca. 6 mo apart yet emerged within ca. 1 mo of each other. Early emerging adults contributed eggs which hatched soon, forming the 2nd generation. This is substantiated by the aforementioned short incubation time of June 1977 eggs from imagos. Thus, this population of *I. sicca*, along with *I. bicolor* (Ide 1935b, Harper and Magnin 1971, Sweeney 1978), *I. japonica* (Ulmer) (Gose 1973) and *I. fattigi* (Smith 1978) was bivoltine. Recruitment was continuous through spring and summer.

The 1st stage nymphs collected during the brief rehydration of Clear Creek in Aug. 1977 probably hatched from mature eggs present in pools or in damp areas beneath the substrate. Larger nymphs present at this time may also have survived the 2 wk dry period in these same areas. However, eggs and nymphs were not found in substrate samples taken during this time. Later pool samples also produced no nymphs, most likely due to the severe stagnation.

Subimagos and Imagos

Isonychia sicca experiences a marked decrease in body size through the emergence period, as indicated by nymphs, subimagos and imagos (Fig. 7,9). The decrease in average subimaginal fecundity from 4440 to 621 eggs/female was also considerable. Comparable decreases in fecundity were found in *Baetis rhodani* (Pictet) (Benech 1972) and *I. bicolor* (Sweeney 1978). Sweeney (1978) hypothesized that temperatures experienced by the nymph during growth affect the number of ovarioles, with higher temperatures resulting in a lower number of ovarioles. Benech (1972) actually correlated decrease in ovariole number through the emergence period with higher temperature. Mayflies with an

extended emergence or bivoltine life cycle commonly experience a reduction in size and fecundity through the emergence period (Ide 1940, Clifford 1970, Pescador and Peters 1974, Sweeney 1978).

Overlap was considerable between the GI-ow and GI-s brood emergences (Fig. 8), and also between the 2 generations. The GI-ow brood contributed to the early emergence, GI-s contributed mostly to the May and early June emergence peaking 6 June, and GII contributed to the late June–early July emergence peaking on 20 June.

Reliable sex ratios were not obtained by light trapping as males dominated the subimaginal ratio (1.4♂:1♀) and females dominated the imaginal ratio (1♂:3.4♀). This change is due mostly to the small number of male imagos captured, as attracted female subimagos and imagos were numerically similar. The low numbers of male imagos caught may possibly be due to increased mortality during the subimaginal stage, high post-mating mortality or differential attraction to lights. Nymphal sex ratio (1♂:1.6♀) appears to be the most reliable estimate since it avoids the problems encountered with the winged stages. Wisely (1965), Clifford (1969) and Corbet et al. (1974) reported a preponderance of females in nymphal populations of other mayfly species.

Recolonization and Diapause

Williams and Hynes (1976a) described 4 methods of stream recolonization: drift, colonization from aerial sources via oviposition, upstream migration within the water and vertical upward migration from within the substrate. We investigated these strategies to determine how *I. sicca* recolonized Clear Creek after dry periods.

During Oct. 1977, while Clear Creek was dry, upstream sites along Clear Creek and its tributaries were sampled for *I. sicca* nymphs which could have potentially recolonized downstream sites by drift. Most upstream sites were similarly dry; a few headwater streams were running but lacked *I. sicca* nymphs. Therefore, we conclude that drift was not a probable recolonization mechanism.

During dry periods, lower reaches of Clear Creek were also dry and could not have provided nymphs for possible upstream migration. Elm Fork was not a source of recolonizing nymphs during the 1978 recolonization of Clear Creek since 1st stage nymphs appeared in Clear Creek 1st. The short longevity of *I. sicca* subimagos and imagos precluded their survival through the dry periods or winters during this study.

Hyporheic burrowing most likely did not occur because of the hard-packed sand beneath the surface rubble, lack of fossorial appendages on nymphs and absence of nymphs in vertical substrate samples. Further support for this comes from Poole and Stewart (1976) who found *I. sicca* nymphs inhabiting only the upper 10 cm of a deep gravel-rubble substrate in the Brazos River, TX. This type of substrate with large interstices would permit *I. sicca* to crawl to considerable depths. However, these interstices began to fill with sand at the 10 cm depth (Rhame and Stewart 1976) apparently limiting *I. sicca* to only the upper layer, although flow and dissolved oxygen may also have limited vertical distribution (Poole and Stewart 1976).

After rejecting nymphal, subimaginal and imaginal stages as potential recolonizers, we believed *I. sicca* survived dry periods in the egg stage. This seemed reasonable since (1) recolonization took place via 1st stage nymphs in Clear Creek; (2) 2 species of stoneflies in Clear Creek have been reported to diapause through dry summers in the egg stage, *Hydroperla crosbyi* (Needham and Claassen) (Oberndorfer and Stewart 1977) and *Perlesta placida* (Hagan) (Snellen and Stewart 1979); and (3) 2 other mayflies *Ameletus ludens* Needham (Clemens 1922) and *Paraleptophlebia ontario* (McDunnough) (Williams and Hynes 1976b), probably survive summer dry periods in the egg stage. We had anticipated this strategy and further suspected that eggs were capable of diapause. Poor success with artificial fertilization experiments and the inability to capture recently mated females precluded our attempts to establish the influence of egg diapause. However, data obtained through sampling could be used to infer diapause. For clarification, we are following Tauber and Tauber's (1979) definition of diapause and Saunder's (1976) definition of quiescence. If *I. sicca* eggs were quiescent through summer dry periods, they would be expected to hatch soon after rehydration. However, comparatively few eggs hatched in fall 1976; most eggs hatched the following spring (Fig. 7). These eggs hatching in spring could be inferred to have diapaused through the summer since they did not hatch after the resumption of normal stream conditions. *Isonychia sicca* may possibly experience a differential breaking of diapause beginning soon after rehydration. Those eggs breaking diapause in early fall may experience temperatures favorable for hatching, while those breaking diapause late fall and winter experience cool temperatures which induce quiescence and delay hatching to warmer spring months. No winter hatching was observed during the 1976–78 study period in Clear Creek or during 1977–78 in Elm Fork.

Diapause in Ephemeroptera has been suggested for *Leptophlebia vespertina* (L.) (Brittain 1972), *Baetis macani* Kimmins (Brittain 1975), *Ephemerella deficiens* Morgan and *E. minimella* McDunnough (Coleman and Hynes 1970), *Ephemera funeralis* McDunnough (Hamilton and Tarter 1977), *Analetris eximia* Edmunds (Lehmkuhl 1976) and *Paraleptophlebia ontario* (Williams and Hynes 1976b), but has been definitively proven through experimentation only in *Ephoron album* (Edmunds et al. 1956), *Baetis vernus* Curtis (Bohle 1969) and *Ephemerella ignita* (Bohle 1972).

In permanent Elm Fork, a large population of nymphs of all size classes was found in Sept. 1977, indicating that eggs probably did not diapause during the previous summer. Hatching continued until Oct., also ceased through winter and resumed in spring. Cessation of hatching during winter may be advantageous to *I. sicca* since decreases in nymphal populations were observed during winter in Clear Creek (1976–77, Fig. 7) and especially in Elm Fork (1977–78).

In summary, we believe that *I. sicca* most likely diapauses in the egg stage through dry periods. Upon usual fall rehydration, eggs slowly break diapause differentially through the fall with those breaking early producing an overwintering brood. Eggs breaking diapause in late fall or winter experience cool water temperatures which probably induce quiescence. Hatching begins again in spring. In a permanent stream, eggs continue to hatch through summer and fall until cool winter temperatures probably induce quiescence, and eggs resume hatching in spring.

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