Population Synchrony in Mayflies: A Predator Satiation Hypothesis

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POPULATION SYNCHRONY IN MAYFLIES:
A PREDATOR SATIATION HYPOTHESIS

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The larvae of mayflies (Order: Ephemeroptera) inhabit most permanent freshwater environments (rivers, lakes, ponds). The duration of the mayfly life cycle varies from a few weeks to several years depending on the response of each species to regional climate and nutrition (Needham et al., 1935). Most of the mayfly life cycle is spent in either the egg or larval stage because almost none of the adults feed and, depending on the species, live only about 10 min to 48 h before reproduction and death. Adults of many species appear in flight in large numbers during a brief period each year and form vast mating swarms over the water surface. Both the size and periodicity of mayfly swarms have been conspicuous enough to stimulate detailed descriptions by early naturalists (see Needham et al., 1935 for review) as well as more recent speculation concerning the ecological and evolutionary significance of swarm periodicity (Corbet, 1964; Edmunds and Edmunds, 1980).

Population synchronization in aquatic insects, especially mayflies, refers to a tendency for the adult reproductive stage of individuals in a given population to be active in the environment during a short, well defined period of the year (i.e., seasonal synchronization within a time frame >24 h but usually less than 2–4 wk) and/or the day (i.e., time frame <24 h and usually about 1–2 h in duration). For our purpose here, each 24-h period represents a unit of observation and the sum of such units describes the emergence period for each species under consideration.

It has been suggested that the adaptive value of adult synchronization for an insect species resides largely with increasing the probability of finding a mate (Corbet,

1964). If so, synchronization should be developed best in species having short-lived adults that are spatially dispersed. This hypothesis is difficult to test because spatial dispersion cannot be adequately determined. In addition, no one has demonstrated for any aquatic species that individuals emerging very early or late in the emergence period fail to mate successfully. Here we argue that mating success is unlikely to have been the only factor selecting for adult synchronization in mayflies. We hypothesize that predator satiation provides a better conceptual framework for assessing adult emergence patterns in mayflies and perhaps other aquatic insects.

"Predator satiation" was used initially to describe the interaction between periodical cicadas (Insecta: Homoptera) and their predators (see Lloyd and Dybas, 1966 for review). Predator satiation occurs when the quantity of a particular prey item (e.g., cicada) at a given point in time far exceeds the potential number that can be taken by a fixed density of local predators (e.g., birds). The predators are satiated and the remaining prey survive to reproduce providing prey densities remain above the level necessary for satiation. Thus, a predator satiation hypothesis for any predator-prey system predicts an inverse relationship between prey mortality due to predation and prey availability above the level needed to satiate predators as long as the number of predators remains more or less fixed for a given time interval.

In this paper we present quantitative data on adult mortality during each day of the adult emergence period for the mayfly *Dolania americana* Edmunds and Traver to demonstrate how emergence

synchrony of the entire population might be adaptive to individuals of the species due to predator satiation. We then present frequency distributions describing the adult emergence of several other species of mayflies to show how the observed patterns are also consistent with a predator satiation hypothesis.

LIFE HISTORY OF
DOLANIA AMERICANA

Dolania americana is a burrowing mayfly known only from coastal plain streams in the southeastern United States (Peters and Peters, 1977). In Upper Three Runs, a spring-fed black-water stream in South Carolina (33°23′N, 81°37″W), *D. americana* is the dominant mayfly species in or on the sandy bottom. Larvae are very distinct morphologically, being highly adapted for burrowing in sandy substrate (Edmunds and Traver, 1959). Gut analysis shows that larvae are predaceous and feed mainly on midge larvae (Diptera: Chironomidae) (Tsui and Hubbard, 1979).

Adult emergence in Upper Three Runs occurs about 0.5 to 1 h before sunrise during the first two weeks of June. The initial winged stage immediately following emergence is usually sexually immature and is called the subimago. Subimagoes molt again into the sexually mature adult stage (i.e., imago). *Dolania americana* females are unusual among mayflies because they never molt into the imago but instead mate and oviposit as subimagoes. Male *D. americana*, however, do molt into the imago just prior to mating. For convenience, in the rest of the paper we refer to subimago females as adult females even though this is technically incorrect.

At emergence, *D. americana* larvae swim to the water surface and transform into the winged stage in about 10–20 sec while floating downstream. Adults fly from the surface for mating, leaving behind the larval exuvia or "molt skin" which continues to float downstream. Exuviae float for at least 30 min and can be collected readily by surface drift nets (≤5 mm mesh). Adult females live only long enough to mate and deposit eggs back into the river (typically

≤5 min). Male emerge, molt again within a few minutes, and then patrol upstream and downstream over a 15–20 m stretch of river in search of females. A male will keep patrolling until it is preyed on by an aerial predator or falls to the river from exhaustion. The entire adult emergence on a given day lasts about 30 min (i.e., between ≈0530 h and 0600 h EDT).

MATERIALS AND METHODS

During adult emergence the upper 25 cm of river water was strained through a 3.2 mm mesh seine stretched across the river. Seines were deployed at three points, about 50 m apart from one another, to delimit for quantitative analysis two 50 m long study reaches. The river was about 15 m wide and 1 m deep in the study area. The number of adults emerging each day from a given reach was measured by counting the number of cast larval exuviae collected in the skimming seine at the downstream end of each reach. The seine positioned farthest upstream prevented exuviae of larvae emerging upstream of our study area from entering our two 50 m reaches.

Seines were lowered into the water about 1 h before sunrise and raised about 0.5 h after sunrise to bracket the emergence period which usually occurs during a 30 min period just before sunrise. Because dead adults float on the surface, the number of adult males and ovipositing adult females in a given reach can also be estimated by drift capture. Of the females that emerge within a given reach, some are preyed on by aerial predators during the brief mating flight and some are killed at the water surface by surface predators (mainly the gyrinid beetle *Dineutes discolor* Aubé). Females killed at the water surface while ovipositing could be distinguished from other spent females because the gyrinid beetles removed and consumed only the abdomen, which contains the eggs, and left the head, thorax, wings, and legs intact (Fig. 1). The number of damaged and undamaged females collected in each seine was compared to estimate adult mortality due to surface dwelling predators. Mor-
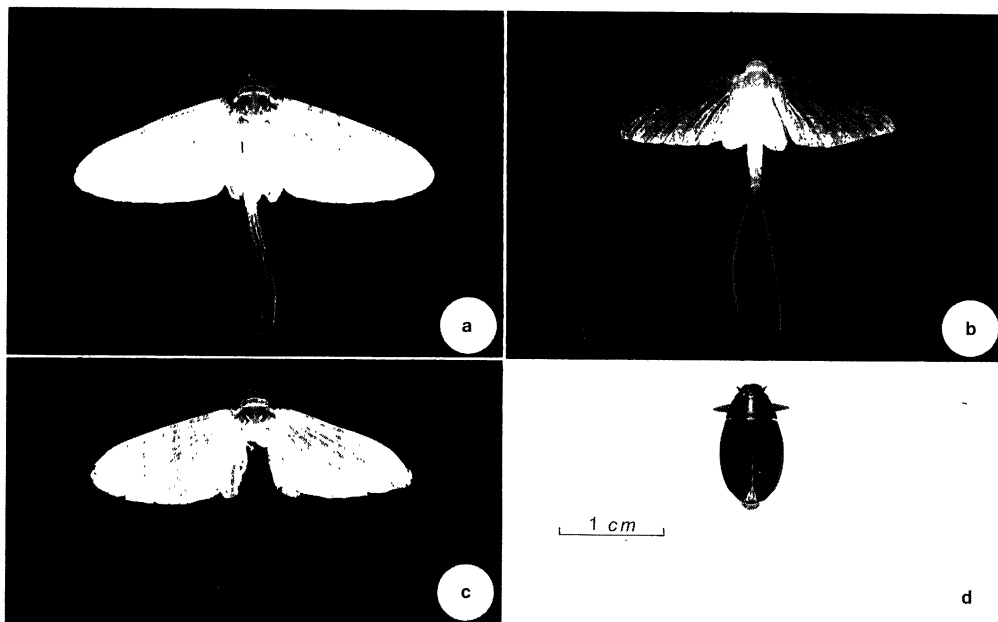
FIG. 1.   a—Female adult of *Dolania americana*. b—Male adult of *D. americana*. c—Female adult of *D. americana* showing loss of abdomen following predation by the beetle *Dineutes discolor*. d—Predaceous adult stage of the beetle, *Dineutes discolor*.

tality from non-surface dwelling predators (e.g., mainly birds and bats) was estimated by comparing the difference between the number of adults (male or female) known to emerge from the reach and the number known to return.

In addition to the three seines, larval exuviae and dead adults were also captured about 40 m upstream from the most upstream seine by drift nets that were deployed off a bridge. These drift nets were also used in 1978 and 1979 to quantify daily emergence and determine the shape of the emergence curve. In 1980 they were deployed simultaneously with the seines and also for a few days after the seines were removed to estimate how much, if any, of the emergence we had missed.

To test the efficiency of our seine method for quantifying numbers of drifting exuviae and adults, we placed plankton nets (500 μm mesh, 0.3 × 0.3 m filter area) in three positions; viz. at the water surface immediately behind the upstream seine, at 0.5 m under the seine, and also at the river bottom. These nets were placed in a cross

sectional area of the river where large numbers of exuviae and adults are usually found in the seine. The surface and bottom plankton nets did not capture a single specimen; the 0.5-m deep net captured one larval molt skin during several days of experimentation. In addition, we lowered our seines on one afternoon and released 89 larval skins just behind the upstream seine. All released skins were found in the next seine downstream when it was raised a few minutes later.

We assumed during our study that adult emigration approximately equalled adult immigration from a given reach each day. The assumption was based on observations that overall adult movement did not appear extensive relative to the size of the study reach (i.e., males generally patrol back and forth over the river as opposed to moving in one direction and females usually mate within a few seconds after emerging from the water surface and immediately oviposit) and the small number of adults observed flying over our seines occurred in both directions. We also as-

sumed that the presence of our seines did not alter the normal flight and mating behavior of adult *D. americana* because males were observed patrolling in normal fashion over our seines and even large obstacles in the river such as natural log jams did not alter the flight behavior.

Adult emergence of *D. americana* was quantified each day by counting the number of larval exuviae in our seines and drift nets on Upper Three Runs. Emergence for all other species discussed in the paper, except *Eurylophella funeralis* McDunnough and *Ameletus ludens* McDunnough, was studied by collecting larvae from White Clay Creek in Pennsylvania (39°53'N, 75°47'W) about one week before the usual emergence date of each species and rearing them in an indoor laboratory stream supplied continuously with fresh stream water. Newly emerged adults were collected daily from vegetation, lights, and the inside environs of the wet laboratory. The timing of adult emergence in the indoor stream is similar to White Clay Creek because photoperiod, temperature, food supply, and water chemistry do not differ significantly in the laboratory stream.

Eurylophella funeralis and *A. ludens* adults were obtained by collecting larvae from a first order tributary of White Clay Creek just before normal emergence and placing the larvae into polypropylene trays (18 cm L, 9 cm W, 8 cm D) that were partially submerged in the stream at the collection site. Each tray had part of its sides removed and replaced with 1 mm Nitex® netting to permit circulation of stream water in the tray. Trays were stocked with detritus and algae for food. A fine mesh net fastened over the top of the tray prevented adults from leaving. Trays were inspected daily for newly emerged adults.

RESULTS AND DISCUSSION

Dolania americana: *Phenology, Population Synchrony, Predation*

Dolania americana has a two year life cycle in Upper Three Runs (Harvey et al., 1980). Eggs are deposited in June and
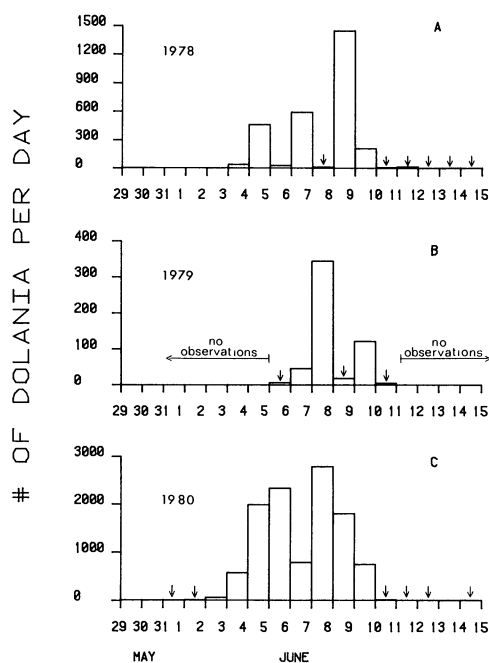

FIG. 2. Total number of cast larval exuviae collected per day during the adult emergence period of *Dolania americana*. A and B—Number of exuviae collected per day in two drift nets. C—Number of exuviae collected per day in two drift nets plus the upstream seine. Arrows indicate dates on which the number of *Dolania americana* were ≤20 and which could not be shown adequately on the scale being used in the figure.

hatch the following April. Larvae require about 14 months to attain maturity and undergo metamorphosis into the winged adult stage. For an individual, the adult stage lasts a maximum of about 0.5 h (female) to 1.0 h (male). For the population, adult emergence usually occurs the first two weeks in June but may be earlier or later depending on how rapidly or slowly the stream warmed during the preceding months (Fig. 2A, B, C).

The number of adults emerging in a given reach per day is highly variable during this period. In 1978 the species exhibited alternating days of low and high numbers of adults (Fig. 2A). Although we missed early and late portions of the 1979 emergence, a pattern similar to 1978 was apparent (Fig. 2B). In 1980 there was one

day (June 6) in the middle of the emergence when few adults were flying but otherwise the alternating pattern was not evident. We have no idea at this time as to what underlying factor(s) might be associated with this day to day variation. We have observed no correlation in past years between the alternating high-low pattern and environmental fluctuations (e.g., water temperature, river stage, rainfall, wind, etc.).

The day to day variation in the size of adult emergence presented a good opportunity for a natural experiment because each day a different number of prey was released into the environment for a short period of time. If the number of potential predators on *D. americana* does not change significantly during the emergence period, then day to day changes in the percentage of adult mortality might be related to changes in the number of available adults.

Aerial predators observed preying on *D. americana* adults included birds (nighthawks and swallows), bats, insects (dragonflies), and spiders. The main aquatic predators were whirligig beetles (Coleoptera: Gyrinidae) that reside in colonies on the water surface at the edge of the river. The emergence, mating, and oviposition activity of *D. americana* attract the beetles out into the main channel where they readily capture adults, mostly females, with their forelegs. Every female that we saw grasped by a beetle was found to be without an abdomen after being released by the beetle. Beetles also attack males that fall into the water from fatigue but usually immediately release the individual without severing the abdomen. Since only some of the attacked males are missing abdomens we cannot assess beetle predation on males.

Fish predation did not appear to be significant during the *D. americana* emergence. Surface disruption, ripples, and/or splashing commonly associated with surface feeding by fish was not observed until sunrise, after the adult activity of *D. americana*. The apparent lack of activity before sunrise by surface-feeding fish (viz. *Lepomis gulosus*, *L. punctatus*, *L. auritus*,

L. macrochirus, and *Enneacanthus chaetodon*) in Upper Three Runs seems consistent with the reported diurnal feeding pattern for these species elsewhere (Pflieger, 1975; Carlander, 1977). Although fish were not collected for gut analysis during the 1980 emergence, we attempted to assess fish predation more thoroughly during the June 1981 emergence. Careful observation by three to four biologists standing in the river reaffirmed the lack of visible signs of surface feeding by fish during emergence and ovipositing of *D. americana*. Heavy rains during the 1981 emergence increased river stage by 60–80 cm and precluded seining fish at the end of oviposition but many (ca. 30 day^{-1}) fish were captured in trap nets placed in the river the night before and removed each day about 2 h after emergence. Stomach contents were examined on all surface-feeding species. About one-half of the examined fish contained undigested or partially digested material which indicated recent feeding. No *D. americana* larvae or adults were observed in these fish. At this time we assume that fish predation on *D. americana* in Upper Three Runs is minimal, if it occurs at all, based on the known feeding ecology of the resident fishes, the 1981 gut analysis data, and four years (1978–1981) of visual observations made during adult emergence.

Beetle predation on Dolania americana

The percent of females preyed on by beetles was inversely related to the total number of females available as prey items on a given day (Fig. 3A and B). We used two separate sources of data for this analysis. First, Figure 3A shows mortality levels as estimated for our entire quantitative study area (i.e., the two 50 m reaches combined). Data were combined because each area exhibited the same relationship and the results could be demonstrated with a single figure. Second, Figure 3B shows mortality levels as estimated for an unknown stretch of river above our quantitative study area. Here we compared the combined numbers of preyed and un-preyed females collected

from our upstream seine and the surface drift nets positioned just in front of the upstream seine. Drift nets and seines were lowered and raised at the same time to facilitate comparison from day to day. The data points for June 7 in Figure 3A and B and June 6 in Figure 3A are missing because a power failure on the evening of June 7 caused our frozen samples to defrost and decompose overnight and we could not differentiate preyed versus unpreyed females. The data point for June 6 in Figure 3A was also lost for the same reason. We continued to collect a few larval skins in our seines after June 9 but were unable to collect any adults. This suggests that aerial predators reduced the availability of D. americana adults as prey for gyrinid beetles to zero.

The inverse relationships between prey mortality and prey availability in Figure 3A and B support a predator-satiation hypothesis. The possibility that these relationships are fortuitous seems remote. In Figure 3B we have superimposed two data points from a pilot study in 1979 where we had the two drift nets and the upstream seine in the exact locations as in 1980. These data do not fit exactly on the regression line but are close enough to lend additional validity to our case.

Although the number of gyrinid beetles in our study area was not quantified, we assume that population levels did not change significantly during the emergence period because: (1) the generation time of gyrinid beetles exceeds the duration of the emergence period and thus an increase in population recruitment as a direct response to increased D. americana availability would be impossible; (2) D. americana emerge in significant numbers both upstream and downstream from our study area, reducing the possibility that beetles gradually migrate from adjacent areas of low density into our study area as the emergence progresses.

Dolania americana: Effects of Non-aquatic Predators

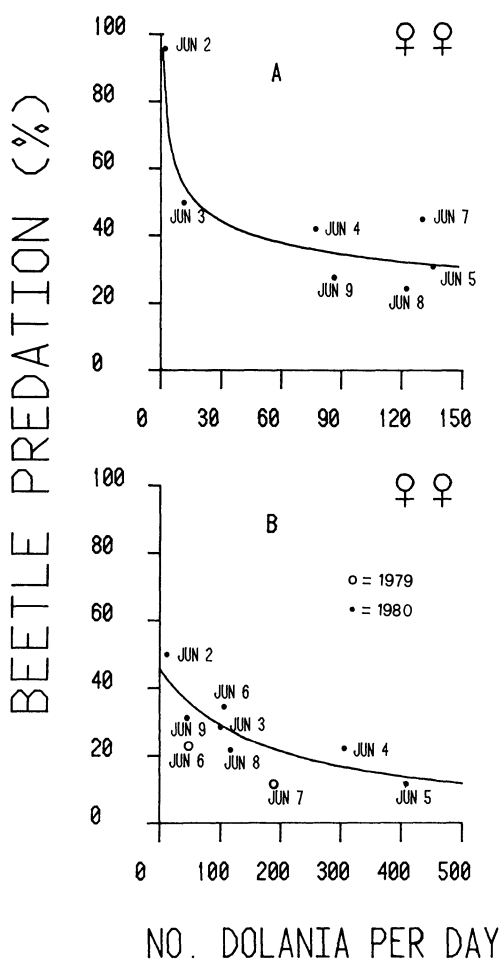An inverse relationship was observed between the percentage of females that

FIG. 3. The percentage of adult female *Dolania americana* preyed on by the beetle *Dineutes discolor* as a function of the total number of female adults present each day for a given reach of river. A—Percent predation for adults captured from the reach of river between the downstream and the upstream seine: $Y = 95.6X^{-0.227}$, $r^2 = 0.79$. B—Percent predation for adults captured from an undefined reach of river upstream from the upstream seine: $Y = 1/(0.0218 + 0.00012X)$, $r^2 = 0.71$. Data points for 1979 were not included in calculating the regression equation.

emerged but never made it back to the water surface and the total number of females that emerged on a given day (Fig. 4A, B, C). We attribute this mortality to aerial predators because, as described previously, fish predation does not seem to be significant on D. americana adults. Pre-
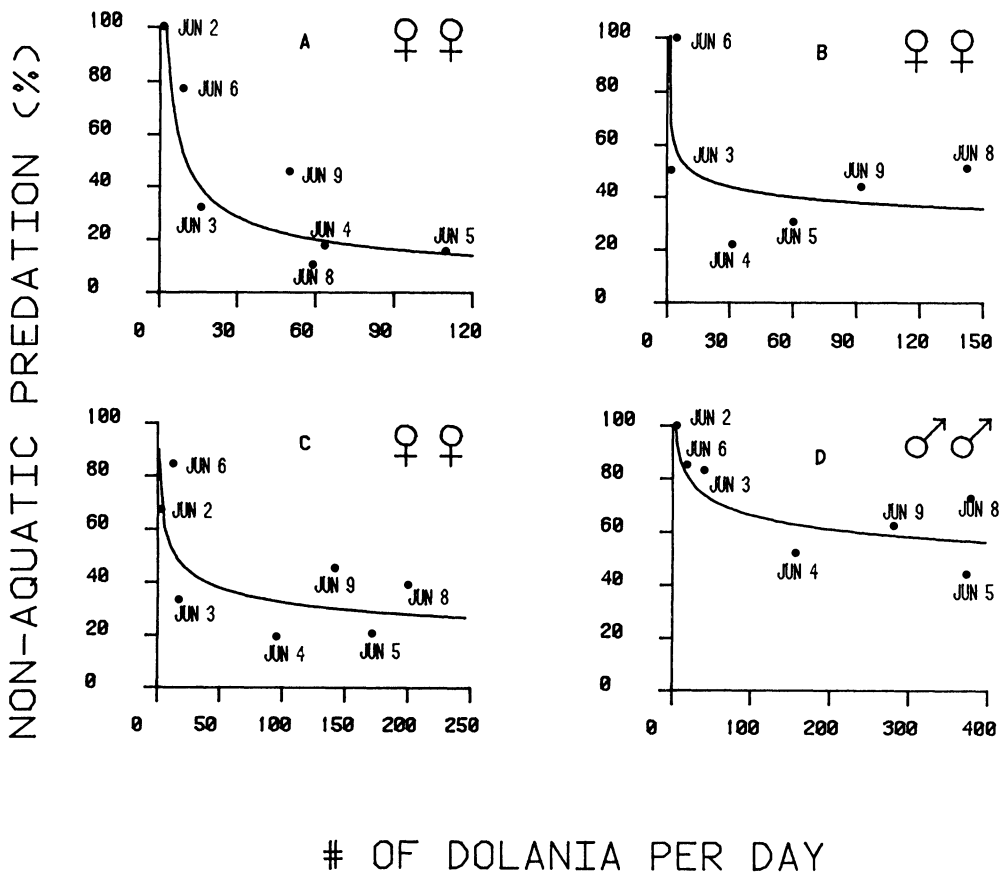
OF DOLANIA PER DAY

FIG. 4. The percentage of adult *Dolania americana* preyed on by non-aquatic predators as a function of the total number of adults present each day for a given reach of river. A—Percent predation on female adults for the reach of river between the upstream and middle seines: $Y = 166.7X^{-0.522}$, $r^2 = 0.71$. B—Percent predation on female adults for the reach of river between the middle and downstream seines: $Y = 67.7X^{-0.132}$, $r^2 = 0.20$. C—Percent predation on female adults for the reach of river between the upstream and downstream seines: $Y = 89.6X^{-0.221}$, $r^2 = 0.42$. D—Percent predation on male adults for the reach of river between the upstream and downstream seines: $Y = 114.9X^{-0.12}$, $r^2 = 0.64$.

dation levels varied from 10 to 100% when each study reach is considered separately (Fig. 4A, B) and from 18% to 84% when our two reaches are combined (Fig. 4C). Estimates of female mortality for a given date were consistently higher for our downstream study reach relative to the reach immediately upstream. The lower number of *D. americana* females emerging per day in the downstream reach may account in part for this pattern, especially if predator density in the two adjacent areas is comparable. Although not shown, we also noticed that female mortality due to beetle predation was equal to or higher for a given day in the downstream study reach relative to the upstream study reach.

The pattern of adult male mortality due to aerial predation was similar to that observed for adult females—viz. mortality decreased with increased size of emergence (Fig. 4D). The magnitude of adult mortality, however, was much higher for males. The higher male mortality undoubtedly results because male adults are exposed to predators for much longer periods of time than females.

We also observed that during days of

large emergence (i.e., when >95 individual males or females emerged in both study reaches combined), adult mortality levels appeared higher than expected after peak emergence (e.g., on June 8 and 9) relative to before the peak (e.g., June 4 and 5). This was observed for both female (Fig. 4C) and male (Fig. 4D) mortality. Although it may be fortuitous and within the random variation of such a study, it may also be related to an increase in "awareness" and/or numbers of aerial predators during the emergence period. The following observations on one aerial predator, a nighthawk, might lend support to the latter idea.

Dolania americana adults began emerging on May 31, 1980 with the first large emergence on June 4. A nighthawk was first observed preying on adults just before the end of the emergence on June 4. It was observed subsequently preying on *D. americana* during each day of the emergence, usually arriving earlier than it had on June 4. On the first day of very low emergence following the peak (June 10), the nighthawk appeared but, after a few passes, it landed for the first time on one of our support posts in the middle of the river and remained stationary for about 1 min while scanning the river with side to side head movements. The nighthawk returned on June 11, 12, and 13 at the appropriate time but after a few passes through the study area at water level, it soon left to feed at and above the forest canopy. This suggests that certain predators may be attracted initially to the *D. americana* emergence by the large number of adults on wing. There may also be a learning process with respect to the timing of maximum prey availability and the efficiency of prey capture such that the number of prey needed to satiate predators may increase during the emergence period.

Others have noted that mass emergence of aquatic insects along a river bank attracts large numbers of non-territorial birds (Martin, 1895 and Lyon, 1915 as cited in Corbet, 1964). As Corbet (1964) points out, this is probably one of several potential drawbacks that might occur from synchronous emergence. Thus, the selective value of mass emergence may in certain situations hang in a fine balance.

Overall Adult Mortality: Males and Females

In this section, overall mortality of females includes death due to both aquatic and non-aquatic predators. For males, beetle predation is not considered because it occurs after the males return to the water (i.e., after the males have mated and completed the reproductive process). Overall male mortality, therefore, is considered equivalent to the estimated mortality due to non-aquatic predators (see Fig. 4D) and is not repeated here.

Overall female mortality for the combined study reaches ranged from 45% to 100% during the emergence period (Fig. 5). Mortality ranged between 45% and 54% on days of large emergence (e.g., >95 individuals). This is somewhat lower than overall male mortality which ranged from 43% to 71% on the same dates (see Fig. 4D). The inverse relationship between overall mortality and emergence size shows that the probability of successful reproduction decreases rapidly when emergence is small. Thus, the relative contribution to overall population recruitment by individuals emerging very early and/or late seems small and an individual maximizes its chance for successful reproduction and causes increased synchrony when it emerges exactly at the peak. This seems very critical to maintaining population synchrony, especially since Lloyd and Dybas (1966) have shown theoretically how a little variation in emergence time can cause even perfect synchrony to dissipate to complete asynchrony within 20 generations if natural selective processes are eliminated. This "decay" of population synchrony occurs theoretically even if one assumes that early and late emergers result initially from phenotypic variation. If early and late emerging individuals are genetically distinct, then the decay would occur even faster.
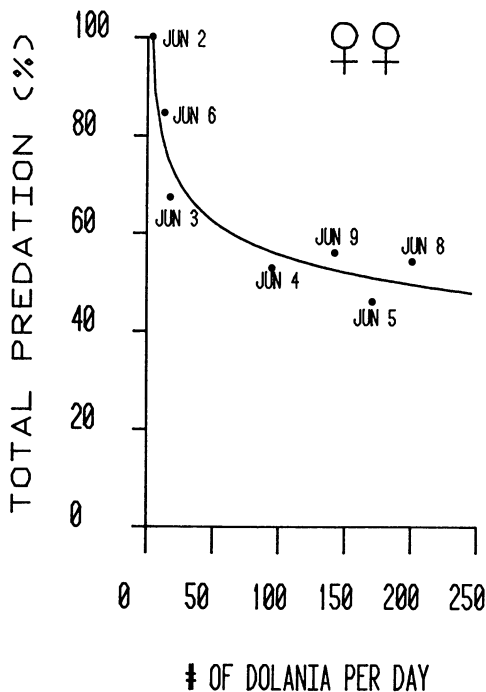
FIG. 5. The percentage of adult female *Dolania americana* preyed on by aquatic and non-aquatic predators combined as a function of the total number of adult females present each day for the reach of river extending from the downstream seine to an undetermined point above our drift nets: $Y = 119.2X^{-0.166}$, $r^2 = 0.91$.

Population Synchrony for Other Mayflies

Figure 6 shows adult emergence curves for several mayfly species in White Clay Creek. Many species have a fairly synchronous emergence lasting 3–4 wk with most individuals emerging during a much narrower period. Peak emergence usually occurs at or before the midpoint in the overall emergence period. Species exhibiting a long emergence period have an emergence distribution skewed to the right as opposed to being skewed to the left (i.e., a number of individuals continue to emerge over a prolonged period of time after the emergence peak—see *Serratella deficiens* Morgan, *Stenonema pudicum* Hagen, *Stenonema modestum* Banks).

Although numerous ecological factors were probably involved to varying degrees

during the evolution of adult synchrony in these species, for this discussion we will focus only on increased probability of successful mating and predator satiation. Increased probability of mating success is intuitively a very reasonable hypothesis concerning the adaptive significance of adult synchrony in mayflies. One approach to evaluating this hypothesis would be to demonstrate quantitatively that a mayfly individual is unable to reproduce or has poor mating success at low densities when shielded from predators. For *D. americana*, we were unable to eliminate predators but we did observe adults mating successfully during days of very low emergence densities. However, predation on ovipositing females was heavy and overall recruitment was probably low on days of low emergence. We know of no quantitative data bearing on mating success at low versus high adult densities for mayflies.

An alternative approach to evaluating the mating success hypothesis is to analyze emergence patterns of parthenogenetic mayfly populations. For parthenogenetic mayflies, the selective disadvantage of emerging early and late would theoretically be lower relative to bisexual populations if a mating success hypothesis were valid. The possibilities that parthenogenesis could lead to a breakdown of synchronized emergence patterns was proposed initially by Corbet and Tjonneland (1955) and Tjonneland (1960) who reported evidence of a temporal dispersal or "decay" in the diel flight activity pattern in certain tropical parthenogenetic species of mayflies. No differences in the degree of adult synchrony for bisexual versus unisexual species were reported for time frames exceeding 24 h. Gibbs (1977), however, suggested that the unusually long (June to November) emergence period of *Cloeon triangulifer* McDunnough is due to its parthenogenetic mode of reproduction. Gibbs (1973) also reported for the same species that at least two distinct summer cohorts usually result because some eggs laid at the end of the previous summer hatch in the fall while others fail to hatch
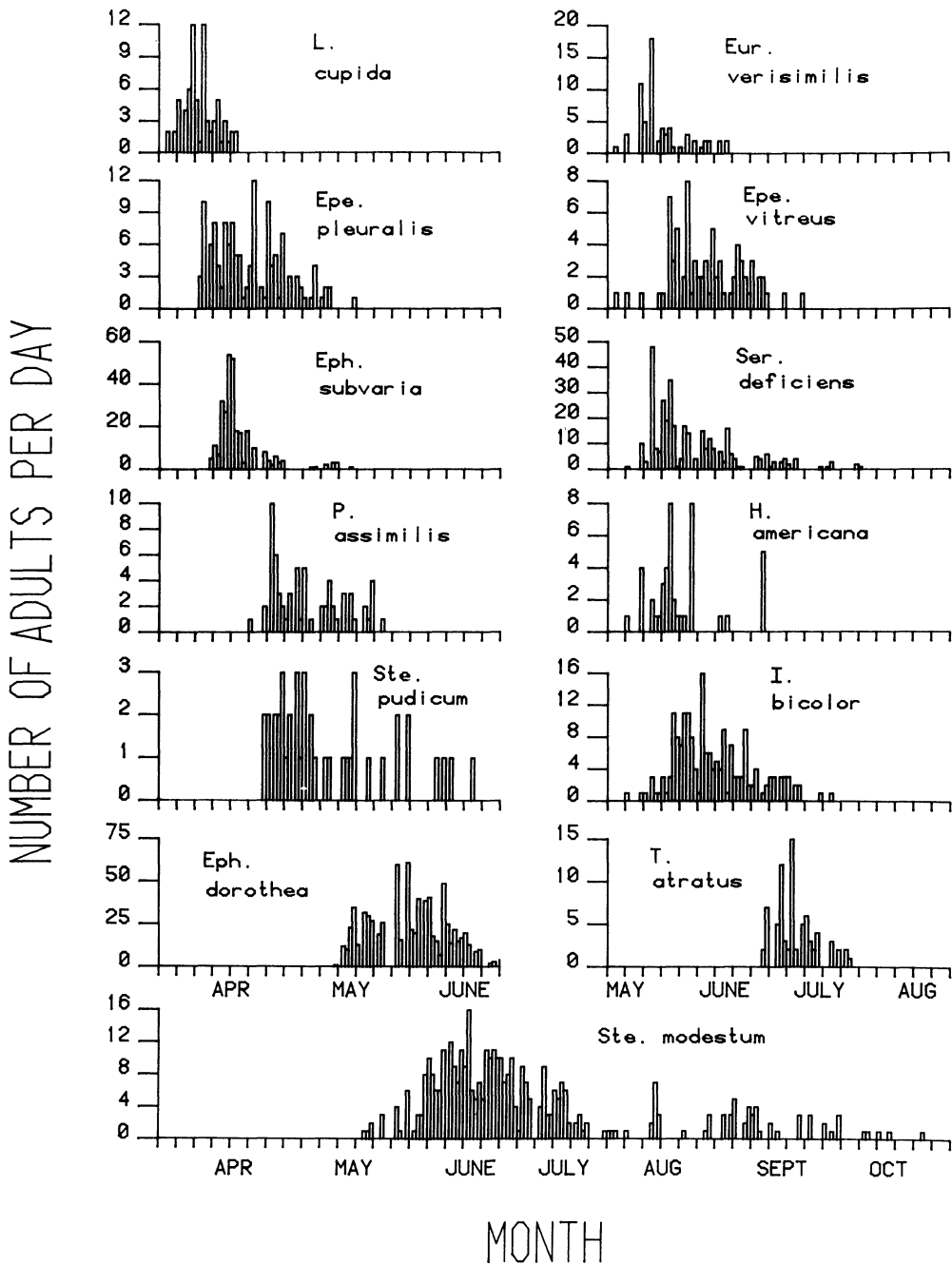
NUMBER OF ADULTS PER DAY

FIG. 6. Adult emergence curves for 12 species of mayflies in White Clay Creek. Each datum per graph is the total number of male and female adults that emerged on a given day. The absence of a datum for a day during the emergence of a species indicates either that no adults emerged or that a collection was not made. The species shown include: *Leptophlebia cupida* (Say), *Epeorus pleuralis* (Banks), *Ephemerella subvaria* McDunnough, *Paraleptophlebia assimilis* (Banks), *Stenonema pudicum* (Hagen), *Ephemerella dorothea* Needham, *Eurylophella verisimilis* McDunnough, *Epeorus vitreus* (Walker), *Serratella deficiens* Morgan, *Habrophlebiodes americana* (Banks), *Isonychia bicolor* (Walker), *Tricorythodes atratus* McDunnough and *Stenonema modestum* (Banks).

until spring. In addition to multiple summer cohorts, the possibility of an additional summer generation seems likely because eggs of the species laid in early summer at White Clay Creek, Pennsylvania, develop immediately after deposition and hatch within a few weeks (unpubl. data). Thus, the emergence pattern may seem non-synchronous because it reflects the adult emergence of several distinct cohorts and/or generations during the summer. We have also observed this pattern of prolonged, continuous summer emergence for several multivoltine species of mayflies in White Clay Creek.

The emergence patterns of parthenogenetic mayflies in White Clay Creek (viz. *Ameletus ludens* McDunnough, *Eurylophella funeralis* McDunnough, and *Cloeon triangulifer* McDunnough) appear to be at least as synchronous as for bisexual species (Fig. 7). Note that only the adult emergence for the first summer generation is shown for the multivoltine *Cloeon triangulifer*. The persistence of a synchronous adult emergence in the three parthenogenetic species suggests that either some factor(s) other than mating success maintains the synchrony or that parthenogenesis has only recently developed in these populations and not enough time has elapsed for disruption of synchrony to occur. We favor the former suggestion but the latter possibility may also have some validity because males have been collected and described for both *A. ludens* and *E. funeralis* in certain localized populations. Over many years we have reared hundreds of specimens of both species in White Clay Creek without finding a male. We do not know, however, how long each population has existed as a parthenogenetic population in White Clay Creek. We know only that our populations have yielded at least 14 parthenogenetic generations in White Clay Creek.

We conclude that adult emergence patterns of parthenogenetic species do not exhibit any "decay" in synchrony and thus do not support a mating success hypothesis for explaining population synchrony in mayflies. We suggest, however, that
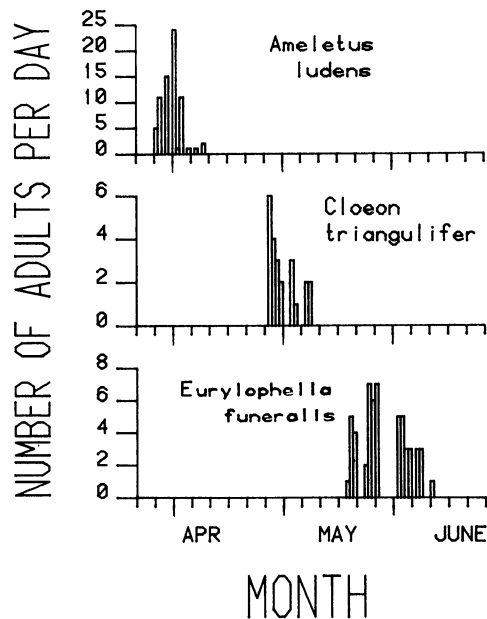

FIG. 7. Adult emergence for three species of parthenogenetic mayflies in White Clay Creek. Each datum per graph is the total number of adults that emerged on a given day.

adult population synchrony is a widespread phenomenon among mayflies and that predator satiation might be an important underlying factor in its evolution.

SUMMARY

Adult emergence of the mayfly *Dolania americana* is highly synchronous, occurring during a two week period in late May or early June. Larvae transform at the water surface into the winged adult just before sunrise during each day of this period. Adults mate, oviposit, and die in less than one hour. Adults are preyed on by both aerial (birds, bats, dragonflies) and aquatic (whirligig beetles) predators. The number of *D. americana* adults that emerge each day can vary by several orders of magnitude due to certain unknown factors. The percentage of adults that succumb to predators, aerial and/or aquatic, on a given day is inversely related to the total number of adults available as prey each day. This inverse relationship supports a predator satiation hypothesis con-

cerning the adaptive significance of reproductive synchrony in this species. Thus, an individual adult *D. americana* maximizes its chance for successful reproduction by emerging synchronously with other members of its own cohort.

Adult emergence data on several other mayfly species are presented to show that reproductive synchrony similar to *D. americana* is widespread among mayflies. An alternative hypothesis concerning reproductive synchrony among mayflies is that the adaptive significance lies mainly with increasing the probability of each sex finding a mate during the brief adult stage. This hypothesis is tested indirectly by comparing the degree of adult reproductive synchrony of three parthenogenetic species with the synchrony of bisexual species. Past workers have predicted that parthenogenetic species should exhibit a decay or loss in reproductive synchrony because selective processes concerning mating success are not applicable. It is shown that reproductive synchrony among parthenogenetic mayflies is equal to or greater than synchrony of bisexual species. Predator satiation is proposed as an alternative factor for future studies on the adaptive significance of reproductive synchrony in mayflies.

ACKNOWLEDGMENTS

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