

To Dr. Hubbard with the author's compliments
N. Watanabe

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Timing of emergence of males and females of *Ephoron shigae* (Ephemeroptera: Polymitarcyidae)

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SUMMARY. 1. The winged adults of *Ephoron shigae* swarming over the water surface were collected by successive random sweeps during their daily emergence period, and the changes in sex and stage composition were examined, in the lower reach of the Asahi River in western Japan.

2. The emergence occurred mainly during a 1½ h period beginning some time after sunset. Male sub-imagos emerged synchronously and moulted to imagos in a 25 min period immediately prior to an abrupt increase of female emergence.

3. This timing of male emergence may be considered the result of selection of males to decrease the risk of death before mating, and for all the males to have an equal opportunity to mate.

Introduction

Mass emergence during mid-September of a burrowing mayfly, *Ephoron shigae* (Takahashi), has been reported in several Japanese rivers where it has caused interference to traffic and sometimes car accidents.

Shioyama (1978) observed in the Kinu River, Tochigi Prefecture, that the winged adults of this species consisted exclusively of female sub-imagos and that they laid eggs as sub-imagos. He also gave some information about their flight time and variation in body size with time of day. Nozaki (1983) also found that all of the winged stages collected in the Sagami River, Kanagawa Prefecture, were female sub-imagos, and he reported the habitat, food and seasonal changes in the size of nymphs, together with morphological features of eggs. Nakamura (1985) and Nakamura *et al.* (1987) maintained eggs from the Kinu River under temporarily cold tempera-

tures, paralleling Britt's (1962) experiments on *Ephoron album*, and showed that more than 80% of the eggs hatched parthenogenetically. However, although the outline of the biology of *E. shigae* is now known, many problems concerning its life history remain unsolved. In particular, there has been no detailed study of the diurnal emergence pattern despite the fact that the synchronous appearance of winged adults after sunset has attracted the attention of many people.

Shioyama (1987) mentioned that males were present in some rivers, but gave no data. In a population of *E. shigae* in the Asahi River, we observed males as well as females in some preliminary observations. In this paper, we report the diurnal emergence pattern of *E. shigae*, paying particular attention to the emergence timing of males and females.

Materials and Methods

The study site was located in the lower reach of the Asahi River near the centre of Okayama

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City (long. 133° 56'E, lat. 34°40' N). The river was about 130 m wide and the current was slow, in general. Mass emergence of *E. shigae* occurred in the middle of September and, at its peak, the entire river surface was covered by the mayfly swarm as far as the eye could see. After swarming, the mayflies fell onto the water surface and died.

The imagos and sub-imagos swarming over

the water surface were collected by random strokes through the air with an insect net of 40 cm diameter at a place about 50 cm deep in water on 17 and 19 September 1988. A twenty-stroke sweep was made every 5 min throughout the duration of swarming. The specimens of *E. shigae* were preserved in 50% ethyl alcohol solution. They were divided into male imagos, male sub-imagos and female sub-imagos, and counted

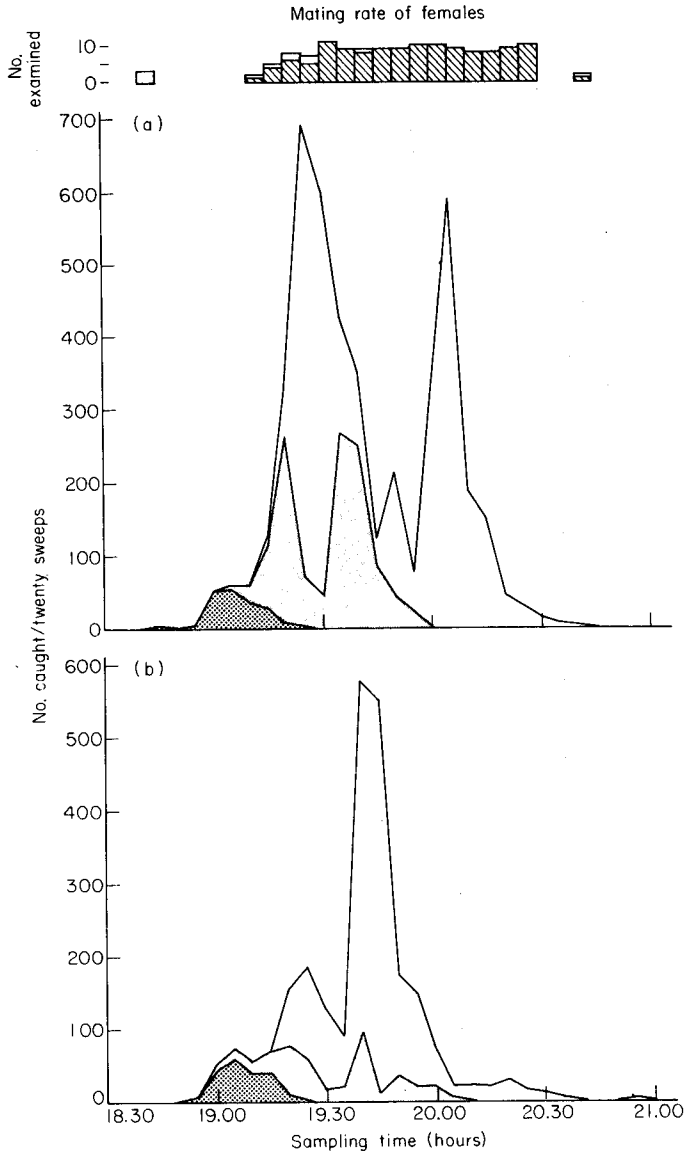


FIG. 1. Diurnal changes in the number of male subimagos (▨), male imagos (□) and female subimagos (□) of *E. shigae* collected by successive random sweeps. The ratio of mated females (shaded) to females examined (open histograms) at each 5 min interval on 17 September is also shown at the top of the figure. (a) 17 September 1988; sunset 18.09 hours; (b) 19 September 1988; sunset 18.06 hours.

in the laboratory. Some moulting individuals were included among the male specimens, but those with long forelegs were classified into imagos and the others into sub-imagos.

On 17 September, the mating rate of the swarming females were checked at 5 min intervals. A part of an egg mass extracted from a female was put on a glass slide with a drop of a linger solution (NaCl 0.9%, KCl 0.02%, CaCl₂ 0.02%, NaHCO₃ 0.002%), and the presence of sperm was checked under a microscope at 150× magnification. As many females as possible were examined within each 5 min interval.

Results

Fig. 1 shows the numbers of male sub-imagos, male imagos and female sub-imagos caught by the insect net from the swarm at successive sampling times on 17 and 19 September 1988. The large majority of *E. shigae* emerged synchronously during an approximately 1½ h period on both days. Male emergence began abruptly at around 19.00 hours. At first, most males were sub-imagos and the proportion of male imagos gradually increased with time. Almost all males had moulted to imagos by the period 19.20–19.25 hours when the number of females abruptly increased. After that, the numbers of male imagos and female sub-imagos fluctuated, probably because the swarming mayflies were not distributed uniformly. Males disappeared from the swarm about 30 min before the females.

The mating ratio of females collected at each 5 min interval on 17 September is also shown in Fig. 1. At a time much earlier than the male emergence, three females were caught by careful searching, but none of them were mated. After 19.25 hours almost all the females collected were mated, at a time when all the males had moulted to imagos. At 20.45 hours, when swarming was coming to an end, one of the two females collected was unmated.

Discussion

The current study confirmed that females of *E. shigae* laid eggs and died as sub-imagos, whereas males developed into imagos, as has also been reported for *Ephoron album* (Britt, 1962) and

Dolania americana whose males emerge well before the females (Peters & Peters, 1977). *E. shigae* males emerged almost synchronously and metamorphosed into imagos during the 25 min period immediately before the large majority of females began to emerge.

Protandry, the phenomenon whereby males emerge a few days earlier than females, is well known in butterflies and other insects (Thornhill & Alcock, 1983). Wiklund & Fagerström (1977) and Iwasa *et al.* (1983) showed, using game theory, that protandry is the optimal strategy for males in species with female monogamy. They argue that protandry has resulted from intra-specific competition for females to mate with. This hypothesis can be applied to the case of *E. shigae*, where males emerge before females during the same day. Although we were unable to observe mating of *E. shigae* directly, sperm was detected in the majority of females collected from the swarm. Males were able to mate immediately with females just after emergence, having already become imagos, and therefore all males had an equal opportunity to mate. Spieth (1940) considered the females of mayflies to be monogamous in general, and males polygamous. Britt (1962) reported that males of *E. album* dropped out of the swarm immediately after they had mated, and expelled their eggs. Peters & Peters (1977), however, often observed several males of *Dolania americana* mating with the same female. Therefore, we cannot definitely conclude that the females of *E. shigae* are monogamous without further observations. However, Wiklund & Fagerström (1977) recognized that protandry could also evolve in species in which the females mate more than once, provided that males which mate with virgin females are favoured. Assuming that the females of *E. shigae* are monogamous, or that if the females are polygamous the fitness of the male which mates after other males is comparatively low, then the emergence time should be determined so that each male may become an imago before the beginning of female emergence. Conversely, a male emerging earlier than others may face a greater risk of death before mating, especially by predation: the observed swarming of *E. shigae* was always accompanied by many bats, *Pipistrellus abramus*. Thus the evolutionarily stable strategy (ESS, Maynard Smith, 1974) for *E. shigae* males is to emerge and moult into imagos synchronously within an extremely short

period immediately prior to the emergence of females.

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