Odonatologica 7 (2): 135-145 *June 1, 1978*

BEHAVIOUR AND BIONOMICS OF *EPIOPHLEBIA SUPERSTES* (SELYS) (ANISOZYGOPTERA: EPIOPHLEBIIDAE). I. DAILY AND SEASONAL ACTIVITIES

T. OKAZAWA and H. UBUKATA
Institute of Zoology, Faculty of Science, Hokkaido University,
Sapporo, 060, Japan

Received February 10, 1978 / Accepted March 31, 1978

Observations were carried out at Hoshioki in Hokkaido, Japan; 1974-1977. Male mating and feeding activities continue from 7:00 to 18:00, while oviposition is restricted to 15:00-19:00. Influences of weather conditions are analyzed. Flight is inhibited by a temperature lower than 12°C. Pre-mating activity of males is suppressed by a temperature lower than 16°C. The reproductive period continues from early June to mid July, with a peak of activities in mid June. The mechanisms and adaptive values of these bionomic features are discussed.

INTRODUCTION

The genus *Epiophlebia* is the sole survivor of the Anisozygoptera and includes only two species. One of these, *E. laidlawi* Tillyard, has long been known, in larval stage, from a Himalayan torrent near Darjeeling. Forty-five years later two adults were collected (ASAHINA, 1963), but virtually nothing is known about its biology. The other species, *E. superstes*, is endemic in the Japanese torrents. Since the publications of ASAHINA (1934) and TOKUNAGA & ODAGAKI (1939) various biological observations have been reported on this species (reviewed by ASAHINA 1948, 1950; EDA, 1966), but there still remain many aspects to be clarified. Since 1974 we have made some observations on *E. superstes*, among which the results on the daily and seasonal activities of adults are described here as the first report. The quantitative field data were obtained by T.O. in 1975, while H.U. participated mainly in bibliographical survey and preparing the manuscript.

STUDY AREA

The observations and the field survey were carried out on the river Hoshioki near Sapporo, a small stream starting at Mt. Oku-Teine (924 m alt.), and emptying into the Japan Sea (cf. OKAZAWA, 1974). The main observation station (320 m alt.) was chosen at a point about 2 km downward from the source of the stream. The station is a section about 30 m long, where the stream is 3-6 m wide, embracing small islets (Fig. 1). Both sides of the valley are steep slopes, about 200 m high, covered by deciduous broad-leaved forests with thick undergrowth mainly of bamboo grasses. At the station the stream is not completely shaded by trees, and the shores are sparsely fringed with willows and densely covered with herbaceous plants, e.g. *Petasites japonicus giganteus* (Fr. Schm.) Kitam., *Polygonum cuspidatum* Sieb. et Zucc., and *Artemisia montana* (Nakai) Pamp.

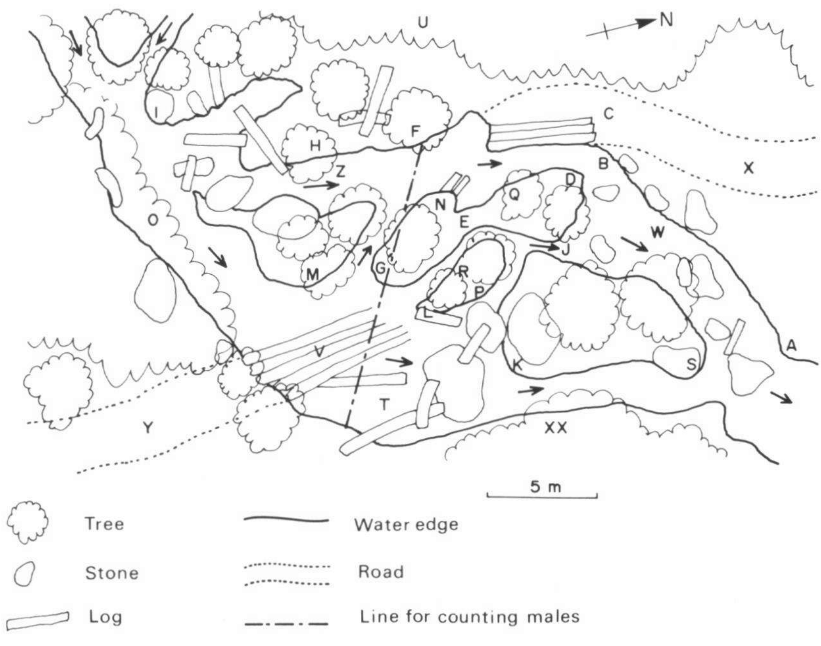

Fig. 1. Topography of the main observation station of the river Hoshioki. F, line for counting flying males; H, site for air temperature measurements; other letters for cross reference in subsequent papers; arrows, directions of the current.

METHODS

In seeking for mates or prey insects, the males of *E. superstes* fly along the narrow mountain-valley without perching (cf. ASAHINA, 1934, 1950). In addition, they neither show residentiality nor defend any area. Such a non-territorial manner is favourable for counting them at a fixed point. The number of flying males both in pre-mating and feeding (henceforth NFM) was recorded at every 30 min at a line drawn transversely on the river in front of point F (Fig. 1). The value of NFM must reflect the relative intensity of activity, though it is not equal to the absolute number of males at Hoshioki. Every female observed within the station was recorded together with its type of behaviour. Meteorological conditions observed at every 30 min were air temperature (measured at a shaded point, H, Fig. 1), amount of cloud, direction and force of wind.

RESULTS

DAILY CHANGE OF MALE FLIGHT ACTIVITY

On June 23, 1975, a day with fine weather, the earliest visit of male occurred at 6:58. As shown in Figure 2, NFM increased promptly after 7:00, and reached a distinct peak at 8:00-8:30. From 10:00 to 13:00, a level of 10-20 was maintained, followed by another peak at 15:30-16:00. Thereafter it decreased gradually till 17:40, after which no dragonfly was seen on that day. From this result as well as those of June 17 and 20, the pattern of daily flight activity on a typically fine day in the middle of the reproductive period can be regarded as a plateau type, occasionally with a weak bimodality.

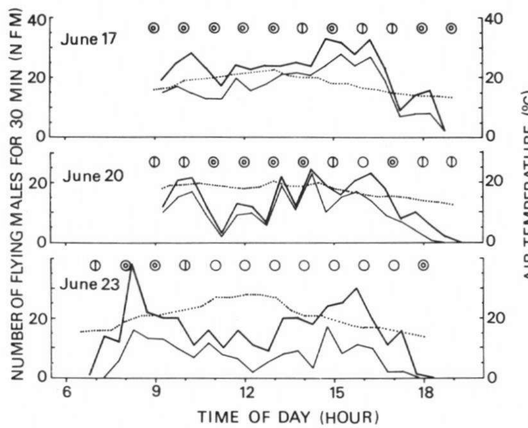

Fig. 2. Daily fluctuation of male activities in June, 1975. Thick line, number of flying males for 30 min (NFM); – thin line, number of males in pre-mating flight for 30 min; – dotted line, air temperature; – O, very fine; ◑, fine; – ◎, cloudy.

INFLUENCES OF WEATHER CONDITIONS ON THE MALE FLIGHT ACTIVITY

T e m p e r a t u r e – The relation of NFM to air temperature, which was measured at the beginning of each census, is shown in Figure 3 with the data of June 20-23. No flight was observed when the air temperature was below 12°C. Flight activity increased with rise in temperature from 13°C to 16°C, but it did not correlate with temperatures higher than 16°C. At a temperature as high as 28°C, the activity seemed to drop slightly, though no significant difference was detected between the average values at medium (16-26°C) and high (26-28°C) temperatures (P = 0.05, t-test). As also shown in Figure 3, no detectable difference was found between before noon and after noon in the response to temperature.

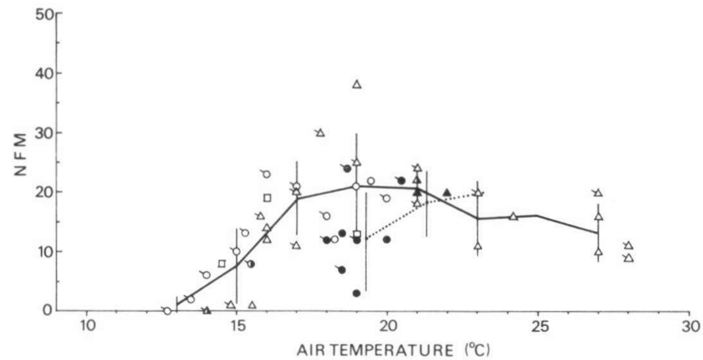

Fig. 3. Relationship of the number of flying males for 30 min (NFM) to air temperature and solar radiation, 1975. Circles, June 20; – squares, June 21; – triangles, June 23; – open symbols, clear weather; – solid symbols, cloudy; – semisolid symbols, slightly cloudy; – oblique bars, data taken in the afternoon; thick line, average value of NFM at every 2°C, clear or slightly cloudy; – dotted line, ditto, cloudy; – vertical bars, standard deviation.

I l l u m i n a t i o n – No accurate measurement of illumination was taken in the present study, but the relative amount and type of the cloud were recorded. For convenience, three degrees were adopted in the analysis: (1) clear, the amount of cloud less than 60%, (2) slightly cloudy, 70-100% cloud, but with the sun strong enough to make shadows, (3) cloudy, 90-100% without shadows on the ground. The response of males to the change of illumination by clouding-up differed between higher and lower air temperatures (Fig. 3). At temperatures higher than 20°C, the reduction of illumination did not influence flight activity. However, NFM was suppressed by reduced light intensity at temperatures below 20°C. The degree of suppression was moderate at 15-20°C, being on the average about half as large as the NFM expected under the clear sky. When the temperature was lower than 15°C, the interception of the solar rays would cause a considerable effect on flight activity. For example, on July 1, 1975, NFM changed from 12 to zero after the sudden strong reduction of the illumination accompanied by the drop in air temperature from 15°C to 14°C. The responses to temperature and illumination were almost the same from June 12 to July 5, 1975.

W i n d – The wind force was recorded on the Beaufort scale, which indicates the relative power of the wind and corresponds roughly with the wind velocity.

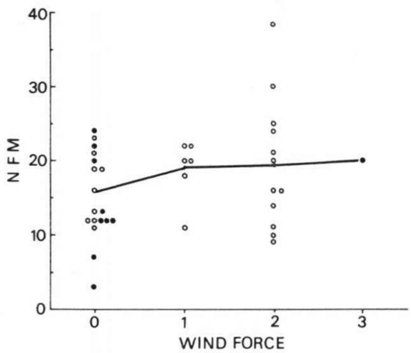

Fig. 4. Relationship of NFM to the wind force on the Beaufort scale (air temperature ⩾16°C), June 20-23, 1975. Line, average value.

As plotted in Figure 4, NFM was not influenced by weaker winds (force ⩽ 3, i.e., slower than 5.4 ms^{-1}) at air temperatures from 16-28°C. At the bottom of a deep valley such as the area studied, we have seldom experienced winds stronger than force 3, so that it is likely that the wind is not the major limiting factor for the flight activity of *E. superstes*, at least in similar habitats.

Rain – A heavy rain, of course, disturbs the flight of most insects. But with light rain, some males continued their flight. A serial observation on June 24, 1974, is cited below:

Time	NFM	Air Temperature	Weather
12:00-12:30	6	15.5°C	cloudy
12:30-13:00	5	16.0	cloudy
13:00-13:30	5	16.0	cloudy
13:30-14:00	6	15.5	light rain

DAILY CHANGE OF THE FLIGHT TYPE OF MALES

The flight of adult males can be divided into two types, viz. feeding and pre-mating flights (cf. ASAHINA, 1950). The former is characterized by a higher level of flight and lack of hovering; the latter by a lower level and the interspersion of distinct hovering. Leaving detailed description and discussion of the behaviour to a later paper, the types are distinguished here by the presence or not of hovering.

Figure 2 shows the daily change in the ratio of the number of males practising pre-mating flight to the total flying males. On June 17 and 20, the ratio was as high as 0.7 during the midday, but it fell below 0.5 after 17:00. On June 23, the ratio was low (< 0.2) in the early morning (6:00-8:00) and in the afternoon (17:00-19:00), while higher (about 0.5) around midday. The relation of this ratio to air temperature (Fig. 5) shows that in mid June the ratio was significantly lower ($P = 0.05$) at air temperatures below 15°C than at 16-25°C, at which it was maintained at higher levels (60-90%). In late June, a similar tendency was recognized, though the ratio decreased as a whole from the level in mid June. On the other hand, the reduction of illumination by cloud did not affect the flight type. Consequently, the behavioural shift from feeding to pre-mating flight or vice versa is likely to be related in part with the air temperature.

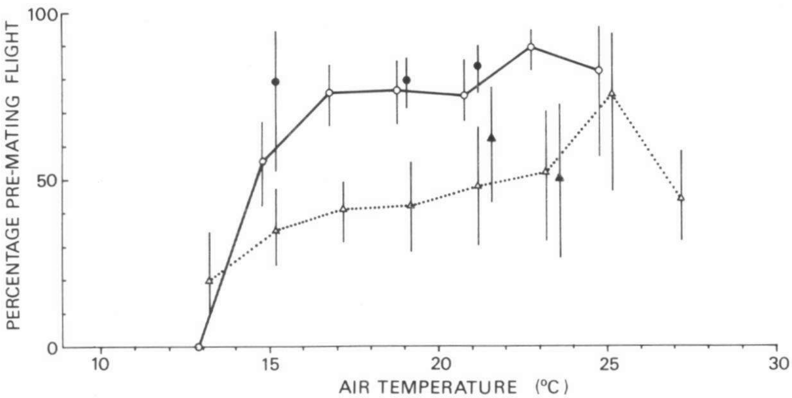

Fig. 5. Relationship of the percentage of males engaged in pre-mating flight to air temperature, 1975. Circles, June 12, 17, 20; – triangles, June 21, 23, 30; – open symbols, clear or slightly cloudy weather; – solid symbols, cloudy; – bars, 95% confidence limits.

FEMALE DAILY ACTIVITIES

The behaviour of females could be divided into five types: (1) oviposition, (2) "false oviposition" (laying posture on the plant stem without actual laying), (3) mating, (4) resting, and (5) feeding. The frequency of observations of these behaviours is shown in Figure 6.

Ovipositions were generally seen from 15:00 to 19:00 except for one case on July 1, 1975; whereas false ovipositions were seen throughout the daytime from 8:00 to 17:00. The mating (tandem formation) occurred from 9:00 to 18:00. This temporal allocation of each behaviour type within the daytime is characteristic of females. Males did not

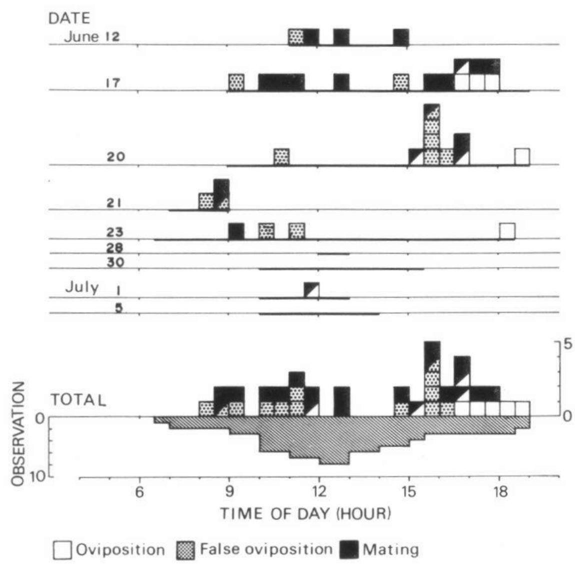

Fig. 6. Daily activities of females (squares), 1975. Hatched bars, total time of observation (hours).

exhibit such an allocation, responding to the air temperature equally before and after noon. An exceptional case observed on July 1 is cited: At 11:37, cloudy with thick cloud and cool (14-15°C), the NFM was very small. A female was perching on a stem of *Petasites* and laying eggs. The number of oviposition holes in which eggs were deposited exceeded 200.

SEASONAL CHANGE OF MALE FLIGHT ACTIVITY

From June 12 to July 5, 1975, each census of NFM was made at an interval of 1-5 days and 3-24 units per day (Fig. 7). The average value was highest on June 12, and thereafter decreased gradually toward July 5, possibly due to the decrease of the adult local population mainly by death. No adult individual was observed during the observation 13:00-16:30, July 25th, while in 1977, a few males were still in flight on July 9th. From these observations, the reproductive period of *E. superstes* probably continues from early June to early or mid July in central Hokkaido.

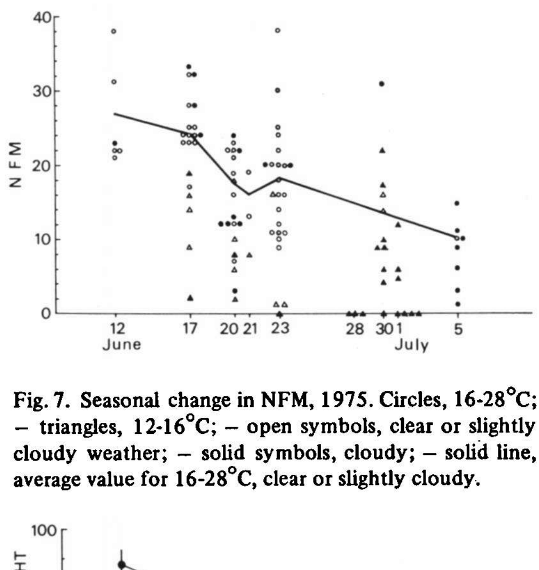

Fig. 7. Seasonal change in NFM, 1975. Circles, 16-28°C; – triangles, 12-16°C; – open symbols, clear or slightly cloudy weather; – solid symbols, cloudy; – solid line, average value for 16-28°C, clear or slightly cloudy.

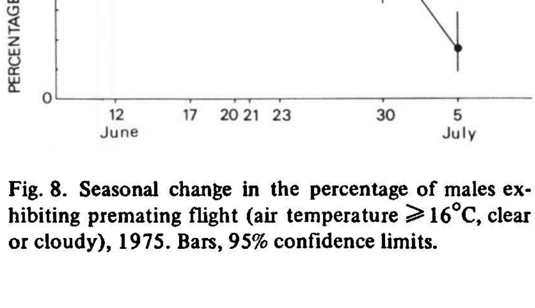

Fig. 8. Seasonal change in the percentage of males exhibiting premating flight (air temperature ⩾16°C, clear or cloudy), 1975. Bars, 95% confidence limits.

SEASONAL CHANGE OF THE FLIGHT TYPE OF MALES

A seasonal change in the ratio of pre-mating to feeding flight was confirmed. The percentage of pre-mating flight was highest (70-90%) during mid June (Fig. 8). The ratio decreased gradually thereafter, reaching 10-30% in early July. This suggests that sexual motivation of males falls with aging. As reported by ASAHINA (1950), the ratio is low also in the earlier days of the flight season.

SEASONAL CHANGE OF FEMALE ACTIVITY

Compared with the number of flying males during a given period of time, that of females was extremely small (cf. ASAHINA, 1934). The sex ratio at the station was 0.3% ♀♀ (n = 1,592) for the census in 1975. Accordingly, tracing seasonal change of female activities is more difficult. Figure 9 shows the seasonal change in the average number of females observed per 30 min. The females

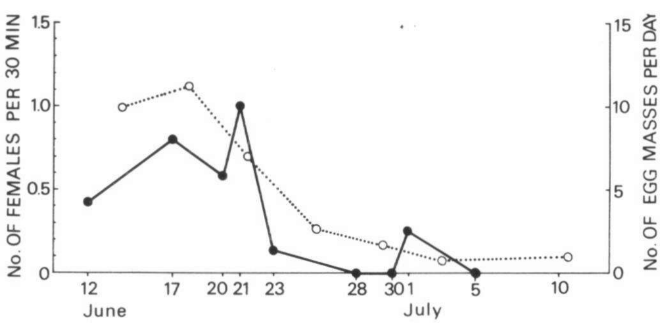

Fig. 9. Seasonal change in the average number of females observed at the station per 30 min (solid line), and that of the number of egg masses laid per day (broken line), 1975.

reached maximum reproductive activity in mid June, it decreased rapidly after June 23, but continued till the beginning of July. As described in another paper, the seasonal change in the number of egg masses laid by females had its peak in mid June, 1975, i.e., coincided well with the above trend.

DISCUSSION

D a i l y a c t i v i t i e s – The pattern of daily activities of *E. superstes* is typically diurnal, as in most of the Temperate Zone dragonflies, except for some crepuscular species (e.g. *Planaeschna milnei* (Sel.); ASAHINA & EDA, 1957). Such a pattern must be caused both by environmental factors, especially climatic ones, and by endogenous rhythms. As stated by CORBET (1962), air temperature is the most important factor among exogenous ones, which is also true for *E. superstes*. On the other hand, illumination seems not to be a limiting factor to the activities at higher latitudes such as Hokkaido, where the minimum daily air temperature frequently falls below 10°C even in June.

The ambient temperature also influences the flight type of males. The ratio of pre-mating flight is reduced by temperatures lower than 16°C. This temperature dependence may be explained by the deduction that reproductive flight requires more heat than feeding flight in Odonata (CORBET, 1962).

An internal physiological rhythm is assumed for the daily activities of females of the population studied, because actual ovipositions were restricted to the late afternoon. Such a restriction of activity to a particular part of the day has seldom been reported in Odonata, except for *Aeshna juncea* (L.) (BARTENEF, 1932), *Mortonagrion selenion* Ris (MIZUTA, 1974), *Pseudagrion melanicterum* Selys (GREEN, 1974), etc. From the evolutionary point of view, the restriction of the time of oviposition to the late afternoon seems to relate to the following conjectures: (1) In *E. superstes* studied, a sufficient amount of food may be needed before oviposition; (2) Disturbance of oviposition by sexually active males may be mitigated by avoiding the time during which the male pre-mating activity is intensive. The latter was supposed also for *Ischnura elegans* (Vander L.) (KRIEGER & KRIEGER-LOIBL, 1958), and is one of various devices to avoid the interference at oviposition, as enumerated by HEYMER (1967) and SAKAGAMI, UBUKATA, IGA & TODA (1974).

According to a personal communication from Dr. S. Asahina, daily activities observed in the vicinity of Tokyo differ from those of Hoshioki in the following characteristics: (1) Feeding flight is seen till about 10:00, whereas pre-mating flight starts at about 11:00 and ended at about 16:00; – (2) The male activities are seldom observed at temperatures as low as 15°C, while they are high at 19-25°C; – (3) Oviposition is not restricted to the late afternoon; moreover, false oviposition is always followed by true oviposition. (1) and (2) seem to indicate that the population of Hoshioki has adapted to lower air temperatures than that of Tokyo. The difference in the time of oviposition is important, because there is no necessity for assuming endogenous rhythm in the females of the Tokyo population.

S e a s o n a l a c t i v i t i e s – The emergence of *E. superstes* takes place between mid April and early May in central Honshu (TOKUNAGA & ODAGAKI, 1939; ISHIDA, 1959). Although emergence was not directly observed in the present study, the emergence season in Hokkaido is presumed as mid May – early June; based on the comparison of flight season between central Honshu and Hokkaido. Furthermore, a relatively high synchronization of emergence is presumed for *E. superstes* by the relatively short flight season. Judged from the seasonal pattern and the possible synchronization of emergence, *E. superstes* is probably a spring species, which has a diapause in the final larval instar, as is known in *Anax imperator* Leach (CORBET, 1957). The emergence season would be determined mainly by adaptation to the annual rhythm of physical environmental conditions such as temperature and photoperiod, though it must also reflect the intra- and interspecific relationships such as predation, parasitism, competition, mating, oviposition, etc. (cf. CORBET, 1962; UBUKATA, 1973).

Nevertheless, the supposed seasonal pattern of emergence in *E. superstes* must provide benefits for the synchronization of both sexes in mating, which would be especially important for a species with a relatively low carrying capacity of population. In addition, the earlier reproductive season must accelerate the rapid growth of the earlier instar larvae during the summer, which may help to increase the survival rate during winter (cf. CORBET, 1957).

The decrease of reproductive activity is synchronized between the sexes, at least in Hoshioki. Oviposition activity is concentrated in mid June, both in the number of females at the station and in the increasing rate of egg mass production. Males fly till mid July without rapid reduction in their density, but the sexual motivation decreases in late June (Fig. 8), simultaneously with that of females.

As regards the bionomic characters of the relic species, *E. superstes*, its daily and seasonal activities do not show any marked difference from those of most zygopterans and anisopterans of the Temperate Zones. This may simply reflect the facts that the Odonata have evolved, in general, as heliophilous insects, and that seasonal regulation is essential to any species which colonized the temperate regions, irrespective of phyletic lines and levels. Primitive features characterizing the life mode of *E. superstes* have been recognized in some habits, and this will be dealt with in a subsequent paper.

ACKNOWLEDGEMENTS

We are indebted to Prof. M. YAMADA and Dr. S.F. SAKAGAMI, Hokkaido University, and to Dr. S. ASAHINA, Tokyo, for their criticism of the manuscript. Cordial thanks are also due to Mr. S. YAMANE, Ibaraki University, for his help in the field.

REFERENCES

ASAHINA, S., 1934. Ecological observations of Epiophlebia superstes. *Kontyu* 12: 103-106. – [Japanese].

ASAHINA, S., 1948. A revised summary of Epiophlebia superstes. *Shin-Konchu* 1: 5-9; 200-205. – [Japanese].

ASAHINA, S., 1950. On the life-history of Epiophlebia superstes (Odonata, Anisozygoptera). *Proc. VIIIth Int. Congr. Ent., Stockholm*, pp. 337-341.

ASAHINA, S., 1963. Description of the possible adult dragonfly of Epiophlebia laidlawi from the Himalayas. *Tombo* 6: 18-20.

ASAHINA, S. & S. EDA, 1957. Oviposition of Planaeschna milnei Selys (Odonata, Aeschnidae). *Kontyu* 25: 81. – [Japanese, with Engl. s.].

BARTENEF, A., 1932. Ueber die Tageskurven des Fluges von Aeschna juncea L. (Odonata) an Hochgebirgsgewässern. *Zool. Anz.* 98: 91-94.

CORBET, P.S., 1957. The life-history of the Emperor Dragonfly Anax imperator Leach (Odonata: Aeshnidae). *J. Anim. Ecol.* 26: 1-69.

CORBET, P.S., 1962. A biology of dragonflies. Witherby, London.

EDA, S., 1966. A living fossil, Epiophlebia superstes. *Kagaku-Asahi* 1966 (April): 83-87. – [Japanese].

GREEN, J., 1974. Territorial behaviour in some Nigerian dragonflies. *Zool. J. Linn. Soc.* 55: 225-233.

HEYMER, A., 1967. Contribution à l'étude du comportement de ponte du genre Platycnemis Burmeister (1839) (Odonata; Zygoptera). *Z. Tierpsychol.* 24: 645-650.

ISHIDA, S., 1959. Ecological notes of Epiophlebia superstes Selys. *Insect Ecol., Tokyo* 7: 103-110. – [Japanese].

KRIEGER, F. & E. KRIEGER-LOIBL, 1958. Beiträge zum Verhalten von Ischnura elegans und Ischnura pumilio (Odonata). *Z. Tierpsychol.* 15: 82-93.

MIZUTA, K., 1974. Ecological and behavioral isolation among Mortonagrion selenion Ris, Ceriagrion melanurum Selys, and Copera annulata (Selys) (Zygoptera: Coenagrionidae, Platycnemididae). *Odonatologica* 3: 231-239.

OKAZAWA, T., 1974. Studies on the aquatic insects in the stream Hoshioki near Sapporo. *J. Fac. Sci. Hokkido Univ.* (VI) 19: 474-488.

SAKAGAMI, S.F., H. UBUKATA, M. IGA & M.J. TODA, 1974. Observations on the behavior of some Odonata in the Bonin Islands, with considerations on the evolution of reproductive behavior in Libellulidae. *J. Fac. Sci. Hokkaido Univ.* (VI) 19: 722-757.

TOKUNAGA, M. & S. ODAGAKI, 1939. Ecological and morphological studies on a dragonfly, Epiophlebia superstes Selys. *Volum. Jubil. Prof. S. Yoshida*, pp. 472-496. – [Japanese].

UBUKATA, H., 1973. Life history and behavior of a corduliid dragonfly, Cordulia aenea amurensis Selys. I. Emergence and pre-reproductive periods. *J. Fac. Sci. Hokkaido Univ.* (VI) 19: 251-269.