CHANGES IN THE SURVIVORSHIP, DISTRIBUTION AND MOVEMENT PATTERN DURING THE ADULT LIFE OF A DAMSELFLY, *LESTES TEMPORALIS*[1] (ZYGOPTERA : ODONATA)

T. UÉDA and M. IWASAKI [2]

Department of Zoology, Faculty of Science, Kyoto University, Sakyo-ku, Kyoto, 606, Japan

Survivorship, distribution and movement of adult *Lestes temporalis* Selys were investigated by marking individuals uniquely in Kyoto, Japan. Emergence began in mid-June and reproductive activity was observed from mid-September. The maximum length of the pre-reproductive period was about 90 days. Most immature adults flew away from water in June and July. In August most adults became residential in the woods. Through these months survival rate for both sexes was extremely high. Before the breeding season started, mature males shifted their distribution sites to water. Thereafter mature females returned to the pond at the beginning of the breeding season. After this they showed a back and forth movement between the pond and the surrounding wood during the breeding season, to oviposit and rest respectively. The survival rate decreased rapidly immediately after the start of the breeding season.

INTRODUCTION

There have been few studies on the ecology of dragonflies during the pre-reproductive period (PAJUNEN, 1962), except for many reports on the length of the period (see VERON, 1973).

Lestes temporalis Selys occurs widely in Honshu, Shikoku and Kyushu Islands in Japan; in continental Asia it has been collected only in the Ussuri basin (ASAHINA, 1956). There are a few published studies of *L. temporalis*: larval growth and a brief note on the life-cycle (AINO, 1934) and a description of oviposition habits and

life history (CHIKUNI, 1953).

The aim of this paper is to show the general trends in the changes of survivorship, distribution and movement pattern through the adult life, including the pre-reproductive period, in *Lestes temporalis*. A detailed analysis and description of reproductive behaviour of the species will be published in a separate paper.

STUDY AREA AND METHOD

The study was carried out on an adult population at the Botanic Garden of Kyoto University, Kyoto City, Japan (Fig. 1). The Botanic Garden is surrounded by buildings and open land, so the population was isolated. During the period from late June to late October we carried out periodic censuses at intervals of three or four days. These censuses involved walking around the census area (Fig. 1), plotting the locations of marked individuals and newly marked individuals on maps of the census area (1/500 scale). *L. temporalis* was marked by placing small spots of fast-drying white lacquer paint on the wings.

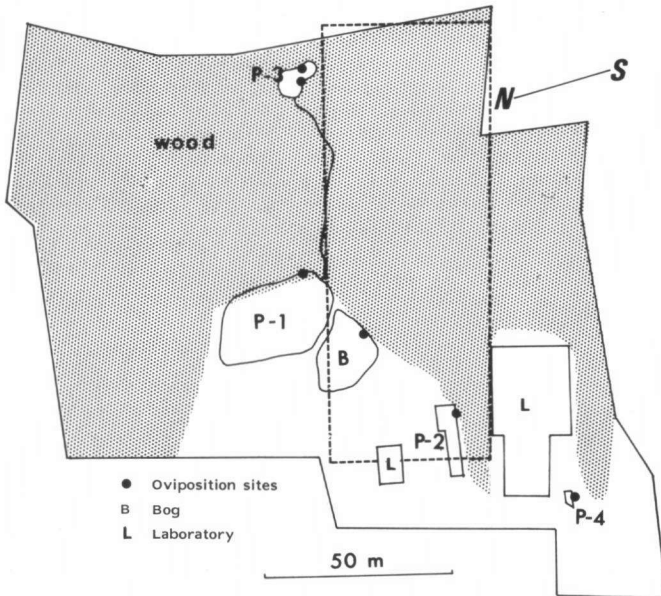From September to October we carried out oviposition censuses

Fig. 1. Schematic map of the Botanic Garden of Kyoto University. This garden has four art-ificial ponds (P-1 to P-4) and one bog. The census area is delimited by a broken line.

on a daily basis, except on rainy days, from 16:00 to 18:00 hours and checked the code numbers of each individual.

Our individual marking system is as follows: A dot indicates a definite number by its position on the wing. If the wing is a right front wing, a spot on the basal part of the costal margin is 1, one on another part of the costal margin is 2, one on the tip of the wing is 4 and one in the middle part of the posterior margin is 7. Thus for the right front wing we can define numbers from one to nine by combining two spots. If the wing is a right hind wing, the spots indicate 10, 20, 40 and 70. Similarly the left front wing gives 100 to 900 and the left hind wing, 1000 to 9000. If four wings are used, we can distinguish 9999 individuals by the combination of spots.

RESULTS

SEASONAL OCCURRENCE AND POPULATION NUMBERS

Lestes temporalis is known to have a long pre-reproductive period in Honshu Island, Japan (AINO, 1934; CHIKUNI, 1953). At the Botanic Garden of Kyoto University, the period of emergence of *L. temporalis* was estimated from mid-June to early August because teneral individuals were caught from June 24 to August 11 in 1976 (Fig. 2).
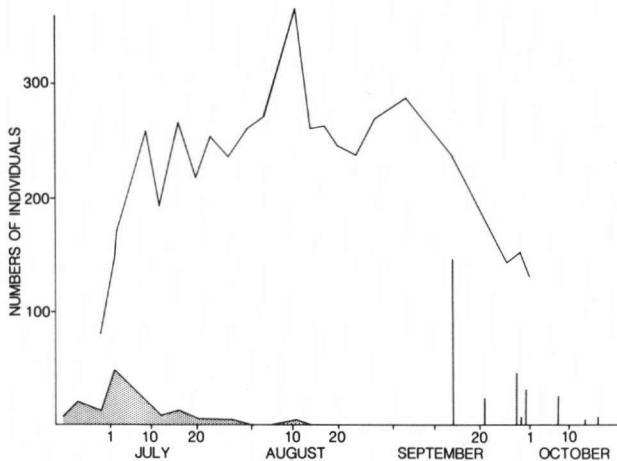

Fig. 2. Seasonal occurrence of imagines and change of population size (estimated by the Manley & Parr method (1968)). Solid line indicates the estimated size of the population (males plus females). Shaded area is number of teneral individuals captured. Vertical bars are numbers of individuals attending oviposition site (including males).

In 1976 the first matings and ovipositions were observed on September 14 (Fig. 2). The start of the reproductive season of the year, however, might have been delayed by continuation of rainy days during early September. In 1975 we observed the first ovipositions on September 4. In any case, some individuals may experience very long pre-reproductive periods lasting about three months, and even the last individuals to emerge may have to spend about one month before the start of the reproductive season.

The estimated population number of adults was about 250 with a rapid increase in early July and a fast decline coinciding with the start of the breeding season (Fig. 2).

SURVIVORSHIP AND LONGEVITY

The survivorship curves for both sexes marked at the teneral stage showed convex shapes (Fig. 3). The daily survival rate during the first 60 days after marking was 0.996 for both sexes excepting the first five days and thereafter their survival rate decreased rapidly, especially for females (Table 1). Most teneral individuals were marked during early July, therefore they may enter the reproductive period about 60 days after marking. This indicates that although the survival rate was very high for both sexes during their pre-reproductive period, the survival rate during the reproductive period was considerably lowered, especially for the females.
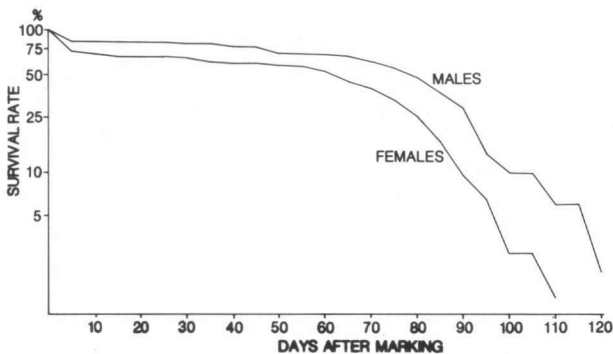

Fig. 3. Survivorship curves for both sexes marked at teneral stage.

The rapid decrease in survival rate observed immediately after marking does not seem to indicate high mortality for teneral individuals, because a similar rapid decrease is observed soon after mark-

Table I

Change of daily survival rate according to age

	1-5	6-60	61-80	81-100
	Days after marking in teneral stage			
Males	0,966	0,996	0,989	0,936
Females	0,933	0,996	0,972	0,925

ing in the mature adults, as shown by the two survivorship curves.

The estimation of individual longevity was based on the length of time between marking and the last recapture of individuals (Table 2). The mean longevity was 78.2 days for males and 68.1 days for females, assuming the apparent high decrease just after marking was the result of a marking effect and omitting this mortality from the calculations. The survival rate during the pre-reproductive period was the same for both sexes, so the difference between the mean longevity of the sexes might be caused by a difference of the activities during the reproductive period.

Table II

Longevity of adults marked while in teneral stage (in days)

	Mean longevity of						Maximum observed survival
	total individuals			those that survived more than six days			
	M	SD	N	M	SD	N	
Males	66.2	35.8	50	78.2	24.5	42	124
Females	49.0	36.8	75	68.1	25.1	53	116

MOBILITY AND MOVEMENT PATTERN

The distances between locations of marked individuals on successive recaptures, measured on census maps, were used to estimate mobility.

The seasonal change of mobility for both sexes is shown in Fig. 4. Both sexes were relatively mobile in July although females were more mobile than males. During this month, movements away from the water (pond P-2) were common for both sexes (Fig. 5).
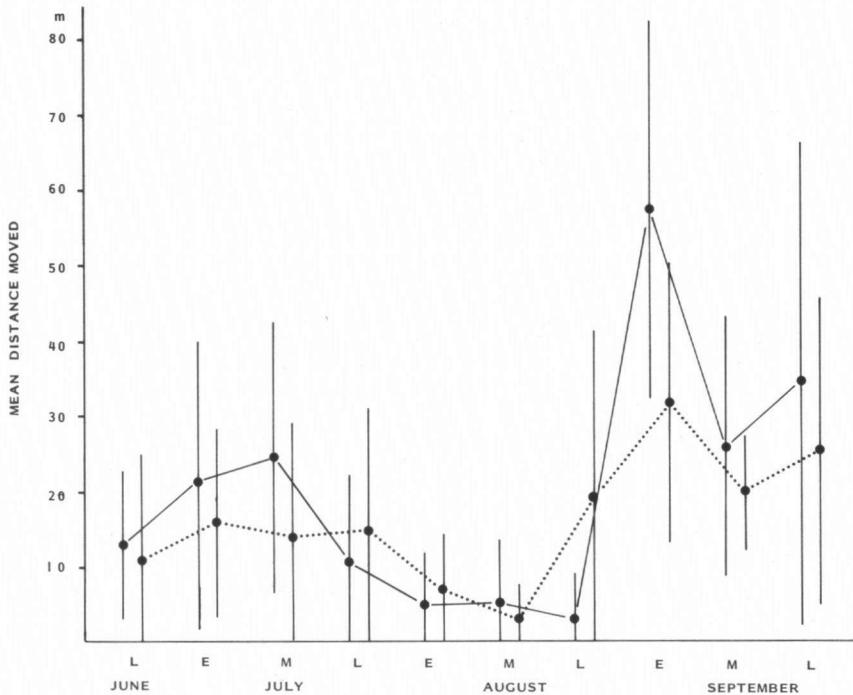
Fig. 4. Seasonal change of the mean distances moved by each sex, calculated for units of ten days, the distance moved by the individual was shared out proportionally to the two units of ten days according to the days spent in each unit of ten days. Dotted line: males; solid line: females; vertical lines: standard deviation.

They became less mobile in August and more than 80% of re-captures occurred within 10 m from the last recapture site of each individual (Fig. 5). They were often found in bushes with densely growing thin twigs. They spent much of their time perching on part-icular twigs and only made short flights less than 20 cm for feeding.

After the relatively immobile period in August, but before the breeding season, males became mobile again. Most of them moved to-ward pond P-2. Thereafter females began to move toward pond P-2 to coincide with the start of the breeding season. The mean distance moved was much longer during the breeding season compared to that during the pre-reproductive period, especially for females (Fig. 4). Frequencies of movements to and from the water were nearly equal in September (Fig. 5). These results suggest that they were con-stantly going back and forth between the pond and the surrounding woods.
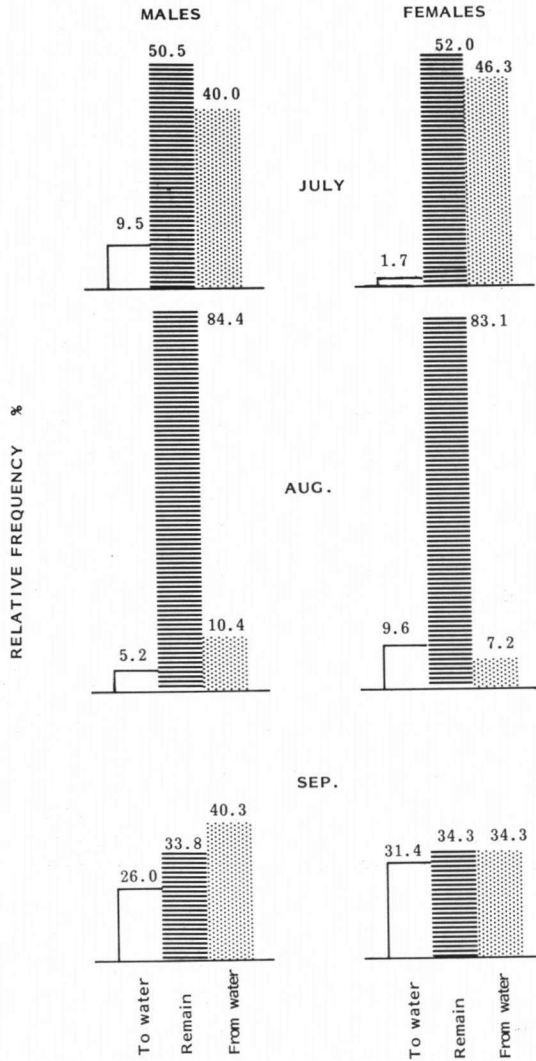
Fig. 5. Seasonal change in directions of movement and residentiality. The word "Remain" means the latest recaptures occurred within 10 m from the previous recapture sites. "To water" means movement toward pond P-2 and "From water" means the reverse movement.
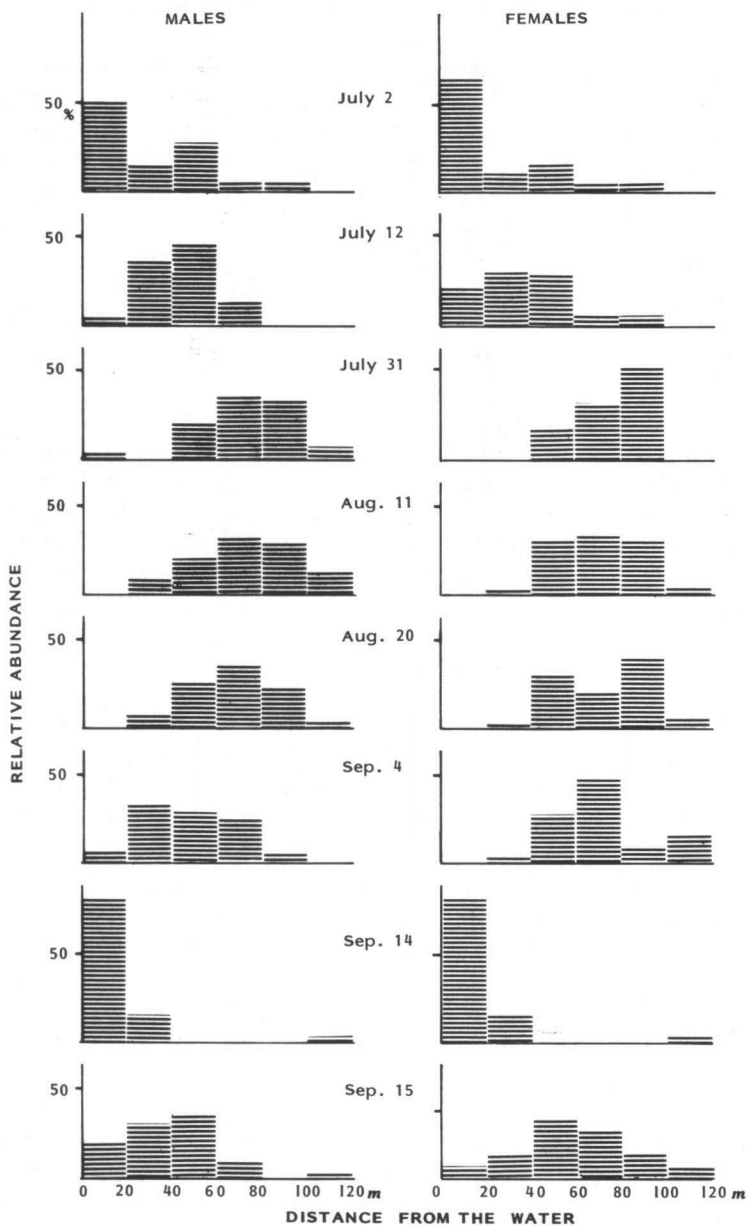
Fig. 6. Seasonal change of the distribution patterns for both sexes. The distribution is shown by the distance from pond P-2 at 10 m intervals. Relative abundance is expressed as percentages of individuals caught in each sector out of the total number caught.

SEASONAL CHANGES OF THE DISTRIBUTION PATTERN

Seasonal changes of the distribution pattern that are expressed by relative abundances of captured individuals according to the distance from the water (pond P-2) coincided with ones expected from the movement patterns (Fig. 6). In early July most individuals remained near the waterside; but later they gradually moved outwards. Both sexes were abundant between 40 m and 100 m from the water in August. In this period both sexes occurred at the same place. Before the start of the breeding season, males moved their sites to the waterside. Males were distributed nearer to the water than females. This difference of distribution pattern between the sexes was maintained through the breeding season.

On September 14, when the first breeding took place, most individuals concentrated at the waterside of pond P-2, and we could not find any individuals in the woods. Next day, September 15, they dispersed over to the woods again. Then most males moved only a shorter distance than females so that during the breeding season male *L. temporalis* occurred near the water (not at the water or waterside) whereas females were abundant at a further distance from water.

DISCUSSION

It is well known that most Lestidae including *L. temporalis* living in the temperate zone are univoltine and overwinter in the egg stage (AINO, 1934; OKUMURA & ISHIMURA, 1938; GARDNER, 1952; GOWER & KORMONDY, 1963; SAWCHYN & GILLOTT, 1974a,b; etc).

In *L. sponsa*, UEDA (1978) found that the prolongation of the pre-reproductive period occurred in the southernmost fringe of the distribution range of the species and suggested that it might be a seasonal regulation of reproductive behaviour in order to maintain the egg stage during winter. In Kyoto, near the southern-most fringe of the distribution range, the maximum length of the reproductive period of *L. sponsa* is about four months.

L. temporalis in Kyoto also had a long pre-reproductive period lasting from one month to three months. There is little information about the life cycle of the species at various localities in the distribution range. It may be considered, however, that the long pre-reproductive period of *L. temporalis* in Kyoto is also a seasonal regulation of their life cycle in order to match the egg stage to winter. From this aspect, it is very interesting to note that the survival rate

during the pre-reproductive period was so high. In order to realise a seasonal regulation of the life-cycle, numbers of the imaginal population have to be maintained until the beginning of the breeding season, by means of a long pre-reproductive period during which reproductive development is inhibited physiologically, and which is spent in an environment conducive to survival. In other words, seasonal adaptation, against geographical variation in environmental conditions may be performed not only by physiological change but also accompanied by ecological change. In *L. temporalis* the very low mortality during the pre-reproductive period may be the main factor that maintains the considerable number of mature individuals till the breeding season. The very low mortality of immature individuals of *L. temporalis* may be related to their life style, since they spend much of their time resting in the bushes under the wood. During this time they are less mobile and thus save much energy, and death due to predation may be reduced as they are all the time resting hidden in the bushes.

During the pre-reproductive period, there was no difference in the distribution between sexes. The males, however, began to move toward water earlier in season than the females when the breeding season approached. As a result of these movements, the males became distributed nearer to water than were the females. Such a difference in the distribution of both sexes was maintained through the breeding season although this resulted from another mechanism : males moved a shorter distance than females between the breeding sites and the wood. The behaviour of males staying nearer to water than the females may be advantageous for their mating success.

It is well known that, in many species of dragonflies, males await the arrival of the females at the favourable oviposition sites and occupy territories. Males of *L. viridis* living in Europe also formed their territories on the top of twigs of trees growing at the waterside and wait for their mates (DREYER, 1978). Although males of *L. temporalis* did not show territorial behaviour and did not concentrate at the breeding sites, it may be said that the mating system of *L. temporalis* is essentially similar to the one exhibited by territorial species.

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