

**POPULATION STRUCTURE OF THE DAMSELFLY  
*CALOPTERYX JAPONICA* SELYS IN AN ISOLATED SMALL  
HABITAT IN A COOL TEMPERATE ZONE OF JAPAN  
(ZYGOPTERA: CALOPTERYGIDAE)**

M. WATANABE<sup>1</sup>, M. TAGUCHI<sup>2</sup> and N. OHSAWA<sup>3</sup>

<sup>1</sup> Department of Biology, Faculty of Education, Mie University, Tsu 514-8507, Japan  
e-mail: watanabe@edu.mie-u.ac.jp

<sup>2</sup> Yaei-Higashi High School, Sagamihara 229-1133, Japan

<sup>3</sup> Kumon Kokusai Junior-Senior High School, Totsuka, Yokohama 244, Japan

*Received May 14, 1997 / Revised and Accepted July 1, 1997*

The population structure was studied in a small stream in a cool temperate zone of Japan in 1989 and 1990, using a mark-release-recapture method. The estimated daily number of males was 500 (1989) and 150 (1990), while that of females was 450 (1989) and 100 (1990). The operational sex ratio in each year was probably unity. The daily estimate number of immigrants in each year was ca. 10% of the population, and the daily survival rate was more than 80%. Therefore, the populations in both years were considered to be closed. The distribution of each individual perching was surveyed. The perching site of the damselfly depended upon the sunlit area on the bank of the stream. Accordingly, they concentrated on the west bank during the morning, and the east bank during the afternoon. However, along the bank the perching sites of males was shown to be a regular distribution, due to territorial behaviour. There were many small insects that could be prey for the damselflies along the stream and the edge of the paddy fields nearby. Dipteran insects were dominant potential prey in this habitat. Since the habitat of the damselfly is surrounded by paddy fields and lakes, the maintenance of the population probably depends upon the abundance of substrate for oviposition and the larval habitat.

**INTRODUCTION**

The odonate fauna on running water in the cool temperate zone of central Honshu, Japan is characterized by species found by small rivers in some plains and in some alpine landscapes. The former habitats are mainly used for rice paddy fields. In

Oh-machi City, Nagano Prefecture, there are several isolated plains surrounded by mountains or hills, and we noticed that four species of Calopterygidae, *Calopteryx japonica*, *C. atrata*, *C. cornelia* and *Mnais pruinosa costalis* are abundant there. The habitat of the damselflies consists mainly of slow-flowing streams with muddy bottoms and such streams service the paddy fields. In the summer, the streams provide a perfect habitat for damselflies, particularly *C. japonica* and *C. atrata*. There is unpolluted water, abundant aquatic vegetation and some shady areas produced by bank vegetation. ISHIDA (1976) pointed out that *Calopteryx* populations often attain high densities.

*Calopteryx japonica* population is restricted to open habitats and after emergence, it stays by the water and shows territorial behaviour when sexually mature (MIYAKAWA, 1983). Immature adults do not leave their emergence sites and as such are atypical (CORBET, 1962). Therefore, each *C. japonica* population seems to be a relatively closed population if suitable habitats are isolated. The immature period is normally the principal dispersal, but the absence of dispersal in *C. japonica* means that the population structure of this species could be intensively studied. However, little attention has been paid to the population ecology of *C. japonica* in Japan, though SUZUKI & TAMAISHI (1981) studied the population parameters of the closely related *C. cornelia*. The reproductive behaviour of *Calopteryx* damselflies has been described by many investigators (e.g. HIGASHI & UEDA, 1982; MIYAKAWA, 1982; WAAGE, 1984; HOOPER, 1995; PLAISTOW & SIVA-JOTHY, 1996).

The aim of the present study was to obtain quantitative information on the adult population structure of *C. japonica*. We used mark-recapture techniques to estimate population size and longevity. The abundance of prey insects was also assessed. Since the mating behaviour was observed during the experiments, the population structure will also help in understanding the *C. japonica* mating system.

#### MATERIALS AND METHODS

Populations of *C. japonica* were studied in an isolated plain of Oh-machi City. The habitat consisted of a small stream (230 m long, 10 m wide), which was relatively straight from north to south because it served as a channel between two lakes (Lake Nakatsuna and Lake Kizaki). Both sides of the stream were surrounded by paddy fields. Towards the south of the stream the small valley with narrow paddy fields continues to Lake Kizaki.

Adults of *C. japonica* fly over the stream from late June to mid August. The aquatic vegetation was abundant and available for oviposition and larval life in 1989 but decreased in 1990. A half of the aquatic vegetation which provided larval habitats was cut off in the spring of 1990.

Adult censuses were carried out along both sides of the stream on mostly clear days for 14 days and 7 days, in late July to mid August of 1989 and 1990, respectively, during which the mating activity of *C. japonica* was considered to be high. It took about 2 hours to patrol one side of the stream. To clarify the distribution of perching sites, visual census was also done from 0500 to 1800 on the 8th August 1989. Plants on the banks were occasionally trimmed by farmers, and the vegetation was about 0.5-1 m tall and the common height of the perching site of *C. japonica* was usually less than 1 m. In

addition, we recorded the number of aggressive flights carried out against other males, the number of copulations and the number of females ovipositing throughout the 8th August 1989.

Adults were captured with a net and mapped. Each was given an individual number that was marked with a white felt-tipped pen on the undersurface of the left hind wing. Every damselfly captured was released immediately at the same capture site after recording the date, site number, sex and age. The marking was considered to have minor effects on their flight activities (and the probability of mating) because most damselflies began to fly normally soon after marking and then to perch. Damselflies wounded during marking were treated as dead individuals in the calculations. The age of the damselfly was estimated into two classes (immature and mature adults), mainly by wing and body conditions, as in the case of the other damselfly species (e.g. WATANABE, 1991). In most populations, the recapture probabilities of the two sexes were different (e.g. WATANABE & HIGASHI, 1989). The sexes of *C. japonica* were processed separately through Jolly's analysis (JOLLY, 1965).

On 8th August 1989, small insects that were regarded as prey for damselflies in the habitat were collected around noon. We used 4 survey lines (50 m in each): inside the emergent plants, above the emergent plants (1.5 m above water surface), above the bank plants (0.5 m above the ground) and above the rice plants (height of rice plant was 0.5 m) next to the bank. This division is related to the real composition of the habitat with different heights from the ground. A plate of A4-size (0.062 m<sup>2</sup>) with a sticky surface was prepared to which small insects would adhere. We moved the plate along each survey line at 5 m/s, that is, we could collect small insects that existed in the space of 3.1 m<sup>3</sup> (=0.062 m<sup>2</sup>×50 m)/10 s. Sampling for each survey line was repeated for 5 times. Each insect adhered to the plate was examined under a microscope (×40) and its body length was measured.

## RESULTS

*C. japonica* passes through one generation per year. As in many calopterygid species, there is sharp behavioural difference between males and females.

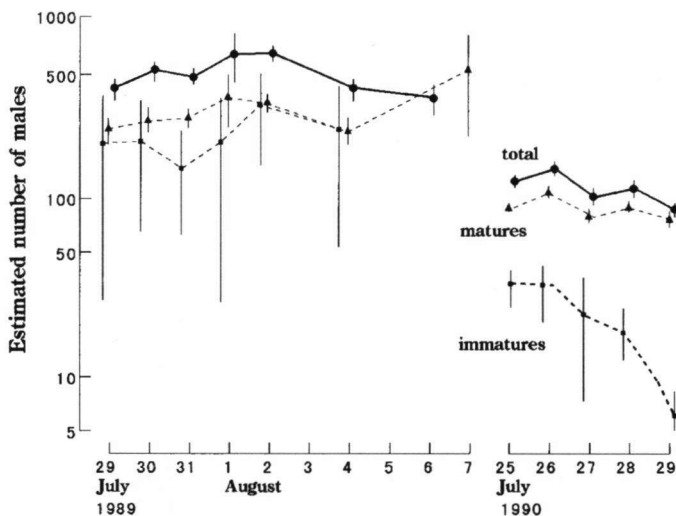


Fig. 1. Changes in estimated daily number of male *Calopteryx japonica* in 1989 and 1990 with those for immature (squares) and mature males (triangles), calculated by Jolly's method. The bars represent standard deviations.

Long-term observations (unpublished) show that males incessantly stay and defend perching sites against rivals, while the females fly about the stream with intermittent feeding, perching and ovipositing. Not only did this cause a relatively small proportion of the females to be marked in the study stream, but the probability of recapturing a marked female was lower than that of recapturing a marked male.

In 1990, there was a shortened emergence period due to little precipitation in the rainy season. Some aquatic vegetation withered due to lack of water, then a half of the remaining aquatic vegetation has been cut and removed by farmers. In addition, 1990 was marked by a severe mid-summer drought with extraordinary high temperatures. Consequently, the drought may have reduced the adult numbers both by interfering with larval growth and by accelerating the ageing of adults.

Adults were found in the whole habitat, but were concentrated on both sides of the stream. These areas supplied adult perching and oviposition sites. Since most adults perched on the plants except during territorial flights, the mark-recapture work was done along the banks of the stream. The adult males defended territories and a few of them were also observed engaged in sneaking behaviour on some days. When sneaking, males did not defend territories but attempted to steal females from other males' territories.

Figure 1 shows estimated population densities of males with their standard deviations (SD). In 1989, there was a relatively constant number of about 200 immature and 300 mature males, respectively. The estimated population size in 1990 was much smaller with roughly 50 immature and 100 mature males, respectively.

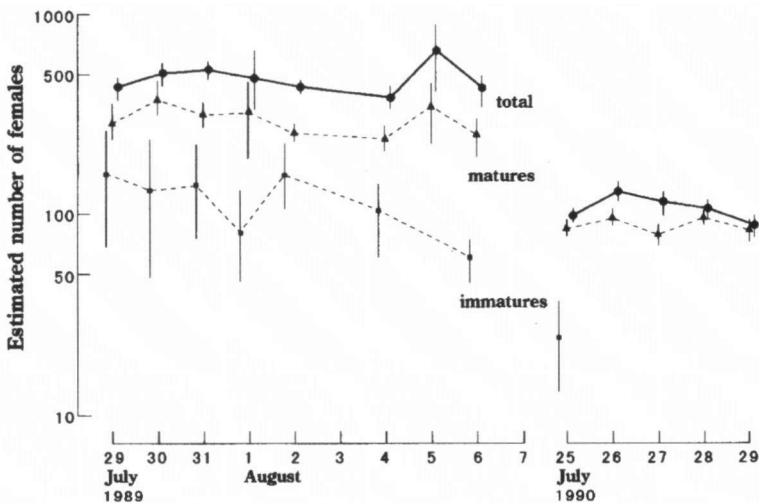


Fig. 2. Changes in estimated daily number of female *Calopteryx japonica* in 1989 and 1990 with those for immature (squares) and mature females (triangles), calculated by Jolly's method. The bars represent standard deviations.

Table I

Estimated daily immigrants, daily survival rates and expected longevity – of *Calopteryx japonica* ( $\pm$  SE)

		Number of immigrants	Survival rate	Expected longevity (days)	
1989	♂	immatures	45 $\pm$ 12 (5)	0.80 $\pm$ 0.07 (8)	5.0
		matures	8 $\pm$ 17 (6)	0.82 $\pm$ 0.09 (10)	5.6
	♀	immatures	19 $\pm$ 20 (6)	0.82 $\pm$ 0.09 (7)	5.6
		matures	12 $\pm$ 29 (7)	0.93 $\pm$ 0.02 (10)	14.3
1990	♂	immatures	1 $\pm$ 4 (4)	0.63 $\pm$ 0.11 (5)	2.7
		matures	6 $\pm$ 1 (4)	0.87 $\pm$ 0.06 (5)	7.7
	♀	immatures	– (0)	1.00 (1)	–
		matures	7 $\pm$ 5 (4)	0.87 $\pm$ 0.05 (5)	7.7

\*: Expected longevity (L) was calculated by the following equation using estimated daily survival rate (S);  $L=1/(1-S)$ .

() : Number of days estimated.

In 1989, the estimated numbers of females were also stable throughout the study, with about 100 immature and 350 mature females, respectively (Fig. 2). Thus, in 1989, the operational sex ratio was close to unity. However, in 1990, we collected a few immature females, most of which matured during the experimental period and none of which were recaptured as immature adults. The estimated daily number of females was about 100.

Table I shows the estimated number of daily immigrants. In 1989, daily immigrants of immature adults were about 1/5 of the estimated daily population for each sex. A few new adults emerged in the survey period, though the survey period was late in the emergence season of *C. japonica*. Therefore, most immigrants may not be true immigrants from other habitats, but new adults emerged in the habitat. The proportion of the daily immigration of mature adults to the estimated population were about 1/30. Most immigrants also consisted of the adults that matured in this habitat, because they already had the individual number marked at the immature stage. There was few true immigrants from other habitats. Therefore, the population was isolated. The similar population trend was also observed in 1990.

Table I also shows the estimated daily survival rate (S) with the rough average of the expected residence rate (L), by the equation:  $L=1/(1-S)$ . The expected residence time was less than 5 days for immature adults, suggesting that it takes about 5 days to sexually mature after emergence. Mature adults may survive more than 1 week. Consequently, the adult longevity of *C. japonica* was more than 2 weeks.

Most male *C. japonica* perched low, near the water surface on the emergent plants, which were open and regarded as a lookout point. Then, mature males occupied the perching site to establish the territory. The perching sites closer to the water surface were defended more aggressively than the others. Most females

perched on the emergent vegetation of the semi-shaded site.

In the morning, only the west bank of the stream receives direct sun light because of eastern high mountains. About 70% of males and about 85% of females perched there irrespective their ages. Around noon, both banks of the stream were exposed to direct sunlight and adults perched on each side of the stream. In the afternoon, the east bank of the stream received direct sunlight due to western high mountains, and about 65% of males and about 85% of females perched there. Both sexes preferred to rest in direct sunlight.

The stream was split into 10 m sections to facilitate recording the location of individuals. Then, the number of sections was 46. The emergent plants for perch-

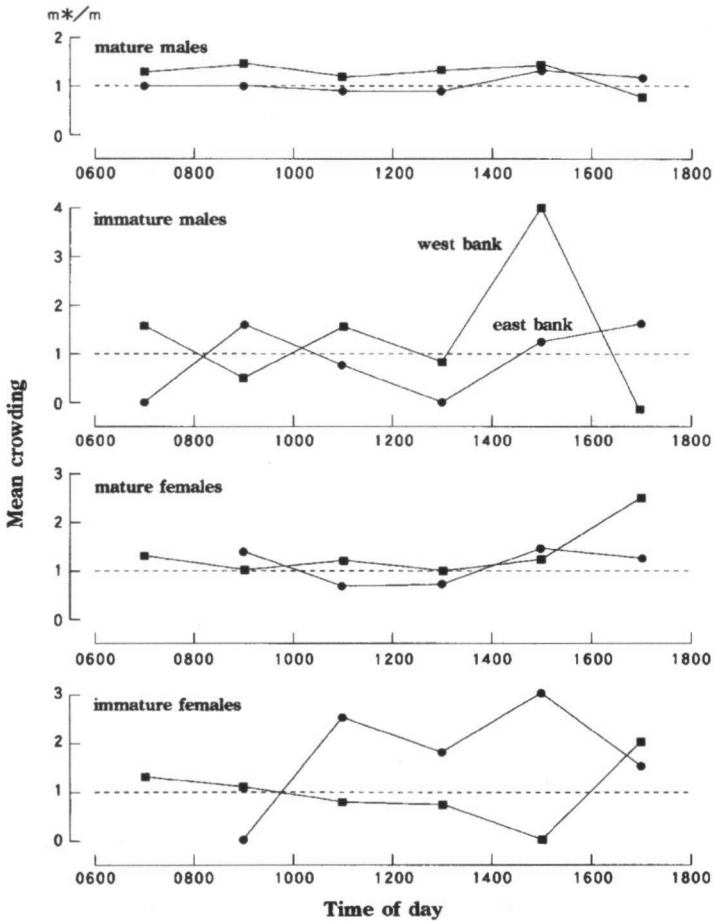


Fig. 3. Diurnal changes in the distribution parameter (mean crowding) of perching sites for adult *Calopteryx japonica* on the east bank (circle) and west bank (square) of the stream. The dotted line shows the random distribution ( $m^*/m=1$ ).

ing and ovipositing were distributed evenly among each section. Figure 3 presents the diurnal change in the  $m^*-m$  index (IWAO, 1968) for both sides of the stream. The distribution of perching site for both sexes was roughly evenly throughout the day, though the population size in each sampling time varied due to the movement of sun mentioned above. In particular, distributions of mature individuals along the bank was random in reproductive hours (0900-1500) during which males showed territorial behaviour expelling their rivals from their perching sites.

The diurnal activity of each sex was counted as the number of flights per hour and the number of mating flights per hour for males (Fig. 4). After sunrise, resting adults on the grass began to be active but the flight activity was weak. The purpose of the flight activity until 0700 was regarded as preying. After 0800, males showed cruising flights, searched their perching site, and then defended. The peak activity occurred around noon, during which tandem, copulatory and guarding behaviours were frequently observed. Oviposition by completely submerged females occurred in living plant material. Take-overs or displacement from the perching site were also observed. In the evening, males exclusively preyed on small insects around their perching site and then rested. Flight activity of females was restricted to preying on small insects and for searching around the resting site, so that their peak

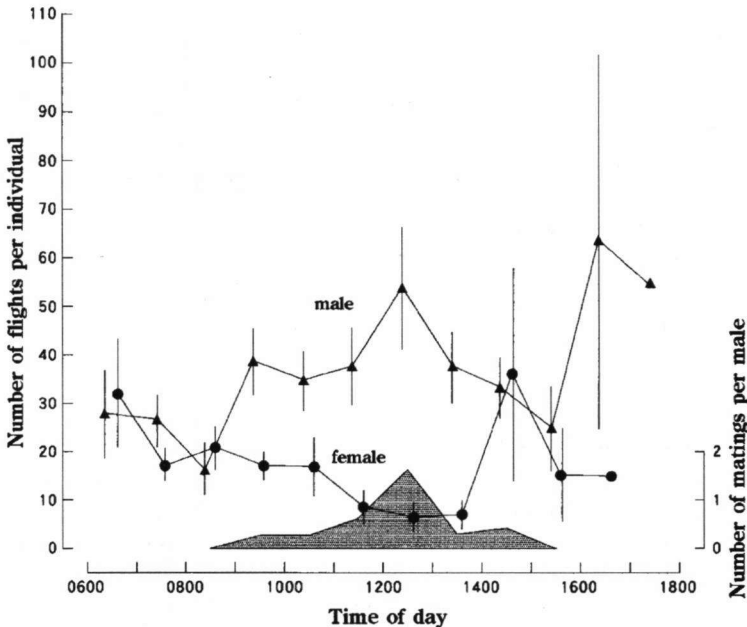


Fig. 4. Diurnal changes in flight activity of *Calopteryx japonica*. Triangles and circles show the number of flights per hour for males and females, respectively. The bars represent standard errors. The shaded area means the number of mating behaviours per male per hour, which consists of tandem, copulating and guarding an ovipositing female.

activity was morning and evening, though reproductive activities were observed around noon.

It was difficult to collect small insects in amongst the emerging plants using the plate with glue due to complex leaves and twigs. However, we collected 18.4 individuals/m<sup>3</sup> on the paddy fields (Fig. 5). The paddy fields along the bank had the largest community among the sample lines (paddy fields - bank:  $\chi^2=9.46$ ,  $0.1>P>0.05$ ; paddy fields - emergent plants:  $\chi^2=18.72$ ,  $P<0.005$ ). The body length of most insects collected was 1-2 mm, which occupied 54% of total insects collected on the bank. Diptera, Hymenoptera and Hemiptera were major insects in this habitat. Although some of the species caught were classified as pest insects of rice, they were regarded as prey insects for *C. japonica*.

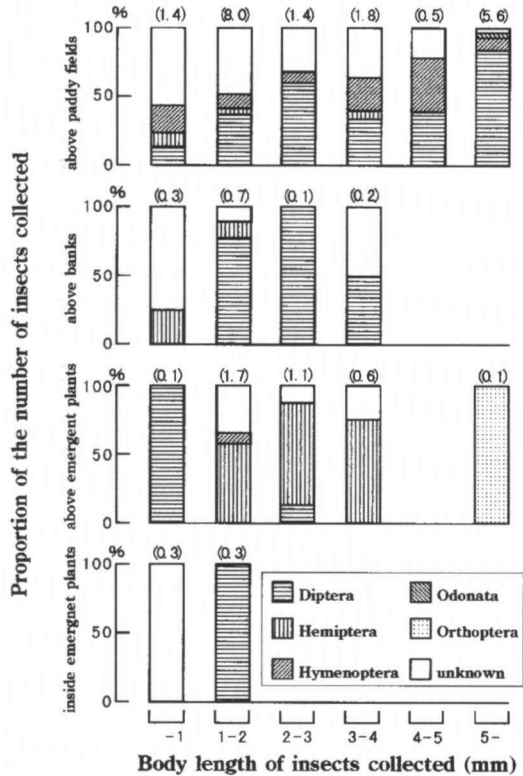


Fig. 5. Communities of small insects collected on the plate in relation to their body size. The mean number of insects adhered to such plate are shown in parenthesis.

DISCUSSION

In many studies on odonate populations, male captures outnumber female captures (e.g. WATANABE & HIGASHI, 1989), because males are present at the breeding site. In the species adopting territorial tactics, particularly, mature males return to water to establish territories but mature females tend to visit only to oviposit. Then, the probability of recapture for territorial males is higher than that for females. Therefore, in odonate species with territorial behaviour variance on estimated male numbers should be lower than that on female numbers. However, in the present study, a considerable number of females were re-captured. Field observations suggest that females tend to stay by water throughout the day. HIGASHI (1976) pointed out that the maiden flights of *C. cornelia* did not disperse immature adults far away from the water from which they emerged, though *C. maculata* is



often considered a forest damselfly (e.g. TAYLOR & MERRIAM, 1996).

The proportion of estimated number of immigrants to the estimated population showed that *C. japonica* has high site fidelity. The operational sex ratio was considered as unity. In many odonate species since females visit by water for reproduction, the prolonged residence by females in the habitat may increase the probability of mating throughout their life span. Although many observations that females can refuse to copulate have been reported, males and females of odonate species are polyandrous. Therefore, females visiting in the reproductive area are regarded as being receptive for mating. Consequently, the operational sex ratio should increase. HIGASHI & UEDA (1982) reported that the sex ratio of *C. cornelia* was approximately 1:1. FORSYTH & MONTGOMERIE (1987) also found an equal population phenology between the sexes of *C. maculata* in Canada. In contrast, the number of females of *M. pruinosa* on a mountain stream was lower than that of males, because the females left the stream after ovipositing (HIGASHI, 1976). An equal sex ratio in the reproductive area was also reported for Anisoptera such as *Sympetrum pedemontanum*, which inhabits paddy fields without any flights away from the fields (TAGUCHI & WATANABE, 1985).

HIGASHI & UEDA (1982) stated that teneral of *C. cornelia* had a tendency to move upstream as is the case with many aquatic insects. CORDERO (1989) also observed a significantly higher tendency to fly upstream in immature than in mature males of *C. haemorrhoidalis*. However, in the present study, Lake Nakatsuna is located upstream of the habitat. Therefore, little movement of females out of their natal area is reflected in the observed stabilities in population structure of *C. japonica*. We did not detect any difference in daily survival between sexes. MIYAKAWA (1982) reported that the mean longevity of *C. japonica* in Saitama Pref. was the same between sexes.

In both the morning and the evening when the ambient temperature decreased to 20°C, adults of *C. japonica* preferred the sunlit area for perching, suggesting that they showed thermoregulatory behaviour, basking. Since the ambient temperature around noon in this study area exceeded over 30°C, the threshold of body temperature to become active might be relatively high. WATANABE (1991) reported that sexually mature males of *Mnais pruinosa* changed the water content of their bodies, whereas mature females did not but they stayed inside the forests to avoid direct sunlight. In the present study, adults of *C. japonica* do not have shady forests available in which to escape the high radiation. They still perched on the sunlit area. Thus, it is possible that a certain thermoregulation system have operated under direct sunlight, open habitat conditions. There are some reports that females of *Calopteryx* spp. submerge to oviposit (e.g. CORBET, 1962). We frequently observed them bathing in the stream, which means that the body temperature must decrease. Such behaviour could make it possible for *C. japonica* to stay in an open area.

WATANABE & MATSUNAMI (1990) showed that the distribution of the male

emerald damselfly, *Lestes sponsa*, was random in the forest floor because they established territories at the sunflecks randomly distributed in the forest. Since male *C. japonica* also established territories expelling their rivals (e.g. AIDA, 1974), the distribution of the perching sites in the banks of the stream must be regular. Abundance of bank vegetation along the stream also supported the regular distribution of the perching sites. Although we did not survey the distribution of perching sites in 1990, cutting off the aquatic vegetation and emergent plants could be caused the distribution pattern of the damselflies to be more clumped. CORDOBA-AGUILAR (1994) pointed out that more aggressive males of *Hetaerina cruentata* were more abundant in substrates closer to the water. The distribution of the female *H. macropus* reflects where they fed rather than where they bred (EBERHARD, 1986).

PIERCE et al. (1985) have made quantitative connections between aquatic vegetation and predation risk of odonate larva from fish. CONVEY (1988) reported that the major advantage of perch possession to *Coenagrion puella* larvae is in the reduction of predation. CORBET et al. (1960) stated that odonate larvae are eaten by a number of freshwater predators including the larger water beetles, some bugs, newts and fish. In the present study, such predators have been identified: for example we found a lot of damselflies inside the stomach of black bass (unpublished). On the other hand, eggs of *C. splendens* placed in fast-flowing water developed significantly faster and showed significantly lower mortality than the eggs placed in slow-flowing water, due to growth of encrusting algae (SIVA-JOTHY et al., 1995). In the study area, however, the harvest of aquatic vegetation might cause a destruction of the *C. japonica* population. It is possible, however, that adult resources might not be a limiting factor, which would explain the relatively consistent large numbers of perching and resting sites by water.

CORBET (1962) stated that adult odonates prey on small insects irrespective of their taxon. HIGASHI (1973) reported that *C. cornelia* quickly responded to every small insect passing through near the perching site. In the present study, most small insects that adhered to the collecting plate might be suitable prey for damselflies. Adults feed on small insects, mainly Diptera and Hymenoptera, and usually stay on the emergent plants or on grasses along the stream bank. Prey insects were abundant in this habitat. Dispersion and behaviour of damselflies of *Calopteryx* species were modified by the size and availability of oviposition resources (MEEK & HERMAN, 1991). Therefore, the quality and the quantity of aquatic vegetation for larval habitats may be more important to maintain the population of *C. japonica* than those of terrestrial vegetation for adults.

#### ACKNOWLEDGEMENTS

This work has been supported primarily by a grant to M. WATANABE from The Foundation for Earth Environment. We are extremely grateful to Messrs. Y. FUKUI, T. HIGASHI, A. ANDO, Y.

NAKANISHI, A. NAGATA, T. KOBAYASHI, T. NAKAMURA, T. HIRANO, K. ISHII and K. SHINTANI for assistance in the field surveys. Special thanks to the anonymous referee for linguistic help.

## REFERENCES

- AIDA, M., 1974. Courtship behaviour of *Calopteryx japonica*. *Insects & Nature* 9(13): 28-30.-[Jap.]
- CONVEY, P., 1988. Competition for perches between larval damselflies: the influence of perch use on feeding efficiency, growth rate and predator avoidance. *Freshw. Biol.* 19: 15-28.
- CORBET, P. S., 1962. *A biology of dragonflies*. Witherby, London.
- CORBET, P. S., C. LONGFIELD & N. W. MOORE, 1960. *Dragonflies*. Collins, London.
- CORDERO, A., 1989. Estructura de tres comunidades de *Calopteryx* (Odonata: Calopterygidae) con diferente composicion especifica. *Limnetica* 5: 83-91.
- CORDOBA-AGUILAR, A., 1994. Male substrate use in relation to age and size in *Hetaerina cruentata* (Rambur) (Zygoptera: Calopterygidae). *Odonatologica* 23: 399-403.
- EBERHARD, W. G., 1986. Behavioral ecology of the tropical damselfly *Hetaerina macropus* Selys (Zygoptera: Calopterygidae). *Odonatologica* 15: 51-60.
- FORSYTH, A. & R. D. MONTGOMERIE, 1987. Alternative reproductive tactics in the territorial damselfly *Calopteryx maculata*: sneaking by older males. *Behav. Ecol. Sociobiol.* 21: 73-81.
- HIGASHI, K., 1973. Estimation of the food consumption for some species of dragonflies. I. Estimation by observation for the frequency of feeding flights of dragonflies. *Rep. Ebino biol. Lab., Kyushu Univ.* 1973 (1): 119-129.-[Jap., with Engl. s.]
- HIGASHI, K., 1976. Ecological studies on the population of *Mnais pruinosa* Selys (Odonata: Calopterygidae). 1. Population density, survival rate and daily activities in the adult damselfly. *Physiol. Ecol. Jpn* 17: 109-116.-[Jap., with Engl. s.]
- HIGASHI, K. & T. UEDA, 1982. Territoriality and movement pattern in a population of *Calopteryx cornelia* (Selys) (Zygoptera: Calopterygidae). *Odonatologica* 11: 129-137.
- HOOPER, R. E., 1995. Individual recognition of mates and non-mates by male *Calopteryx splendens xanthostoma* (Charpentier) (Zygoptera: Calopterygidae). *Odonatologica* 24: 347-352.
- ISHIDA, S., 1976. *Insects' life in Japan*, Vol. 2: *Dragonflies*. Hoikusha, Osaka-[Jap.]
- IWAO, S., 1968. A new regression method for analyzing the aggregation pattern of animal populations. *Res. Popul. Ecol.* 10: 1-20.
- JOLLY, G. M., 1965. Explicit estimates from capture-recapture data with death and immigration-stochastic model. *Biometrika* 52: 225-247.
- MEEK, S. B. & T. B. HERMAN, 1991. The influence of oviposition resources on the dispersion and behaviour of calopterygid damselflies. *Can. J. Zool.* 69: 835-839.
- MIYAKAWA, K., 1982. Reproductive behavior and life span of adult *Calopteryx atrata* Selys and *C. virgo japonica* Selys (Odonata: Zygoptera). *Adv. Odonatol.* 1: 193-203.
- MIYAKAWA, K., 1983. Mating behavior of *Calopteryx* spp. *Insects & Nature* 18(9): 2-7.-[Jap.]
- PIERCE, C. L., P. H. CROWLEY & D. M. JOHNSON, 1985. Behavior and ecological interactions of larval Odonata. *Ecology* 66: 1504-1512.
- PLAISTOW, S. & M. T. SIVA-JOTHY, 1996. Energetic constraints and male mate-securing tactics in the damselfly *Calopteryx splendens xanthostoma* (Charpentier). *Proc. R. Soc. Lond. (B)* 263: 1233-1238.
- SIVA-JOTHY, M. T., D. W. GIBBONS & D. PAIN, 1995. Female oviposition-site preference and egg hatching success in the damselfly *Calopteryx splendens xanthostoma*. *Behav. Ecol. Sociobiol.* 37: 39-44.
- SUZUKI, K. & A. TAMAISHI, 1981. Ethological study on *Calopteryx cornelia* Selys (Odonata, Calopterygidae). I. Analysis of adult behavior by marking-reobservation experiments. *J. Coll. lib. Arts, Toyama Univ. (Nat. Sci.)* 14: 25-40.

- TAGUCHI, M. & M. WATANABE, 1985. Ecological studies of dragonflies in paddy fields surrounded by hills. II. Diurnal behavior of *Sympetrum pedemontanum elatum* Selys. *Rep. environ. Sci. Mie Univ.* 10: 109-117.-[Jap., with Engl. s.]
- TAYLOR, P. D. & G. MERRIAM, 1996. Habitat fragmentation and parasitism of a forest damselfly. *Landscape Ecol.* 11: 181-189.
- WAAGE, J. K., 1984. Female and male interactions during courtship in *Calopteryx maculata* and *C. dimidiata* (Odonata: Calopterygidae): influence of oviposition behaviour. *Anim. Behav.* 32: 400-404.
- WATANABE, M., 1991. Thermoregulation and habitat preference in two wing color forms of *Mnais* damselflies (Odonata: Calopterygidae). *Zool. Sci.* 8: 983-989.
- WATANABE, M. & T. HIGASHI, 1989. Sexual difference of lifetime movement in adults of the Japanese skimmer, *Orthetrum japonicum* (Odonata: Libellulidae), in a forest-paddy field complex. *Ecol. Res.* 4: 85-97.
- WATANABE, M. & E. MATSUNAMI, 1990. A lek-like system in *Lestes sponsa* (Hansemann), with special reference to the diurnal changes in flight activity and mate-finding tactics (Zygoptera: Lestidae). *Odonatologica* 19: 47-59.