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COMMUNITY STRUCTURE OF COEXISTING *SYMPETRUM* SPECIES IN THE CENTRAL JAPANESE PADDY FIELDS IN AUTUMN (ANISOPTERA: LIBELLULIDAE)*

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The mark-recapture method was used for 9 coexisting spp. in Kanagawa (Oct., 1981-1984). In the 4 paddy fields studied, *S. parvulum, S. eroticum* and *S. darwinianum* (in 2 fields) were dominant resp. in downstream direction. Mating occurred mainly in the morning, and the flying activities decreased during the afternoon. *S. parvulum* and *S. eroticum* covered short distances during a day, while *S. darwinianum, S. frequens* and *S. baccha* had low recapture rates, suggesting larger flight distances. In the hills, the community structure was more complex than in the paddy fields, though the population density was lower, and no mating behaviour occurred there. Consequently, the hills are considered to represent the *Sympetrum* roosting area. The paddy fields community structure in Oct. depended on the extent of the available habitats.

INTRODUCTION

Studies on the Anisoptera fauna have been reported in various habitats (e.g. MOORE, 1953, 1964; BENKE & BENKE, 1975; RUDOLPH, 1978; JOHNSON et al., 1980; ARTHINGTON & WATSON, 1982; CROWLEY & JOHNSON, 1982). An abundance of information exists on qualitative aspects of odonate ecology, such as descriptions of life histories (e.g. SAKAGAMI et al., 1974; UBUKATA, 1974). However, quantitative field data necessary for understanding odonate community structure are scarce. The present paper attempts to integrate the quantitative aspect of community structure with the mark-re-

* Ecological studies on dragonflies in paddy fields surrounded by hills. V.

capture method for a group of *Sympetrum* species, coexisting in paddy fields of central Japan in autumn.

S. parvulum, S. e. eroticum, S. darwinianum, S. pedemontanum elatum, S. frequens, S. baccha matutinum, S. infuscatum, S. croceolum and *S. r. risi,* were recorded in paddy fields around Anakawa-Yato, Kanagawa Prefecture (TAGUCHI & WATANABE, 1984). The last two were rare and the others were common. It is generally known that many *Sympetrum* species fly over a wide range, including paddy fields (e.g. MIZUTA, 1978; TAGUCHI & WATANABE, 1985, 1987), though TAGUCHI & WATANABE (1985) reported that the diurnal whereabouts of *S. pedemontanum* are restricted to the paddy fields throughout its adult life.

A life history characterization of each species is essential to the understanding of odonate community structure. All of the paddy field *Sympetrum* seem to hibernate at the egg stage and to hatch in early May, the germination time of rice. BAN & KIRITANI (1980) and URABE et al. (1986) pointed out that odonate larvae appear to be important predators of insect pests in paddy fields. Such dragonfly species might develop synchronously throughout larval stages as if they were a single species (BENKE & BENKE, 1975). Upon emergence, however, the development of *Sympetrum* is more asynchronous, as suggested by TAGUCHI & WATANABE (1984). Temporal partitioning among sympatric species were also reported in other dragonfly species (e.g. MILLER, 1982).

In this paper, adult *Sympetrum* coexisting in paddy fields were studied simultaneously in order to gain an understanding of community structure as well as single-species population dynamics.

STUDY AREA AND METHODS

The experimental paddy fields (6.5. ha) were surrounded by hills, covered mainly with secondary deciduous forest. Four study sites in the paddy fields and a subsidiary one in the hills were selected before the mark-recapture samplings were conducted (Fig. 1). Each site was indicated by a letter.

Site D (ca. 11,720 m^2) was the largest area, and was adjacent to an extensive open paddy field eastwards. Site M (ca. 8,910 m^2) was located around a junction of a main stream and a branch with natural bogs. Site R was in a cul-de-sac (ca. 1,560 m^2). Site G, which was the smallest paddy field, included small bogs (ca. 1,020 m^2) and was completely isolated from the other sites. The hills with deciduous forest lie around site G. The shortest sunlit period in a day, due to the shadow of such hills, was observed at site G. Site U (ca. 2,030 m^2) in the hills was an open deforested area in 1978.

Rice reaping is carried out during early October in the paddy fields. TAGUCHI & WATANABE (1986) reported that, due to rice reaping, the behaviour of *S. frequens* was different in early and late October, but none of the other species showed any change in flight behaviour.

The number of adults found within each area was counted mainly on each holiday (5 or 6 days) of October, from 1981 to 1984. On each sampling day, all individuals found during 15 min periods, from 9 a.m. to 5 p.m., were captured by net and marked on their hind wings with a felt pen. The condition of the wings, as well as that of the abdomen, was recorded. Individuals wounded by marking were treated as dead in this study.

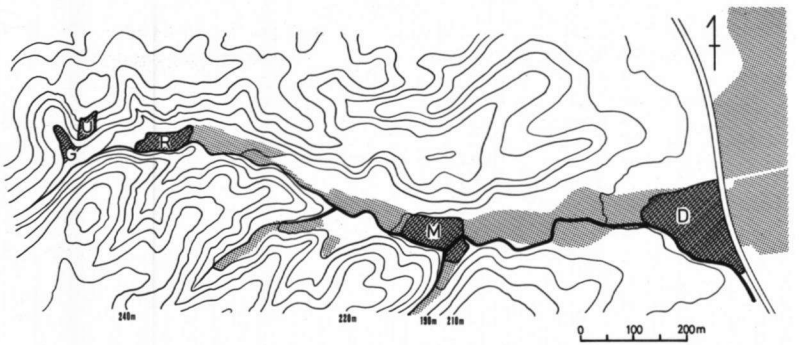

Fig. 1. Study area: Anakawa-Yato, Kanagawa prefecture, Honshu. G, R, M, D and U are the study sites. Shaded area represents the paddy fields.

RESULTS

SPECIES COMPOSITION AND POPULATION DENSITY

All of the 9 recorded species (TAGUCHI & WATANABE, 1984) were captured in October, 1981 to 1984. Most of the males were mature individuals, judging from the red colour of the abdomen. Most of the females were also mature, because their thorax coloration was powdery red and, due to oviposition, in some species mud adhered to parts of the abdomen. Some individuals perched on rice leaves, while others made freqent hovering flights. All of them made intermittent feeding flights, sometimes repeatedly using the same perch, and showing weak interactions.

Since the seasonal trend in the number of individuals in October was similar in each year, the figures for each respective study site were averaged (Tab. I). Six species appeared in each study site every year, and they mated and oviposited in the paddy fields. *S. infuscatum* was rare at any site during the season. One male of *S. croceolum* and one male of *S. risi* were found in 1981 and 1983, respectively, though the number of sampling days was not equal each year.

In the 4 paddy fields, the dominant species were *S. parvulum, S. eroticum, S. darwinianum* and *S. darwinianum,* in site G, R, M and D, respectively. Few *S. parvulum* were flying in site D, which was a relatively open paddy field area. Most *S. parvulum* captured in site M were immigrants from the shady natural bogs southwards. The habitat of *S. parvulum* seemed to be restricted to the paddy fields with shaded areas. *S. eroticum* also preferred the paddy fields with shaded sections, but seemed not to select site G, the most shaded paddy fields, as *S. parvulum* did. *S. darwinianum* preferred open paddy fields. *S. frequens* also seemed to do so, though its density was low, because its local breeding season is

Table I

Mean number (± SE) of *Sympetrum* individuals observed per day in October, 1981-1984 in five ecologically different study areas — (n = number of sampling days)

Species	Sex	G		M				U	
		n	No.	n	No.	n	No.	n	No.	n	No.
parvulum	♂	9	58.9±12.2	14	14.9±4.3	12	41.8± 7.2	6	0.0± 0.0	6	8.2±2.0
	♀	9	8.3± 3.1	14	3.4±0.7	12	5.8± 1.3	6	0.2± 0.2	6	10.0±2.1
eroticum	♂	9	16.2± 2.0	14	67.9±1.0	12	91.9±13.0	6	42.0± 7.0	6	22.2±5.4
	♀	9	9.0± 1.8	14	15.4±3.4	12	12.1± 1.9	6	4.3± 1.5	6	17.5±3.7
darwinianum	♂	9	5.9± 3.2	14	28.4±8.8	12	128.8±16.0	6	133.0±37.7	6	7.7±1.7
	♀	9	19.3± 8.6	14	27.2±8.7	12	92.0±16.9	6	84.5±32.7	6	18.3±3.8
pedemontanum	♂	9	3.3± 1.4	14	15.3±4.8	12	12.1± 2.5	6	20.5± 3.4	6	1.0±0.4
	♀	9	3.4± 1.0	14	6.0±1.6	12	12.3± 1.6	6	16.7± 3.6	6	3.8±1.4
frequens	♂	9	6.1± 3.0	14	11.6±3.6	12	9.3± 3.0	6	3.7± 1.2	6	7.3±4.4
	♀	9	5.2± 1.3	14	9.6±3.2	12	12.8± 3.1	6	4.3± 1.4	6	7.3±3.4
baccha	♂	9	1.6± 0.6	14	4.4±0.9	12	10.3± 2.1	6	0.7± 0.4	6	0.7±0.3
	♀	9	1.0± 0.3	14	2.1±0.5	12	4.3± 0.9	6	1.0± 0.4	6	1.0±0.4
infuscatum	♂	9	0.2± 0.1	14	0.0±0.0	12	0.4± 0.1	6	0.3± 0.2	6	0.3±0.2
	♀	9	0.1± 0.1	14	0.0±0.0	12	0.2± 0.2	6	0.3± 0.3	6	0.0±0.0

not until November (TAGUCHI & WATANABE, 1986). Similarly, as the local breeding season of *S. pedemontanum* falls mainly in August (TAGUCHI & WATANABE, 1985), its density in October was also low. Most individuals of *S. pedemontanum* were more aged than those of the other species, and they seemed not to appreciate site G. The tendency that both the most shaded and the most open paddy fields were not considered attractive was also noticed in *S. baccha,* the density of which was low.

Since the paddy fields are the *Sympetrum* breeding habitat, the mating process and oviposition behaviour of each species must determine the species-specific sex ratio (cf. UBUKATA, 1974; TAGUCHI & WATANABE, 1984). An excess of males was found in both *S. parvulum* and *S. eroticum.* The sex ratios of *S. darwinianum, S. pedemontanum* and *S. frequens* in the respective paddy fields of their preference were estimated at roughly 1:1.

In the hills (site U), the dominant species was *S. eroticum.* The *Sympetrum* hill community appears to be the most complex among the sites studied. The population density was lower than in the paddy fields. It was noticed that the sex ratio was roughly equal or biased to females in all of the hill species. None of these showed any mating behaviour.

DAILY ACTIVITY PATTERNS

Since the hourly changes in the number of individuals were similar each year, the data were pooled in the respective species (Fig. 2). In the paddy fields, the highest densities of most species occurred in the morning. In the evening, most of them had been away from the paddy fields. Such a daily pattern was found in *S. parvulum, S. eroticum* and *S. darwinianum* at sites G, R and D respectively. Each of them was the dominant species at the respective site. No discrepancy of the activity pattern was observed between sexes, despite the fact that in some species, the female density was lower than that of the males. In the hills (site U), on the other hand, there was a weak tendency towards a higher morning activity and a decrease in the afternoon.

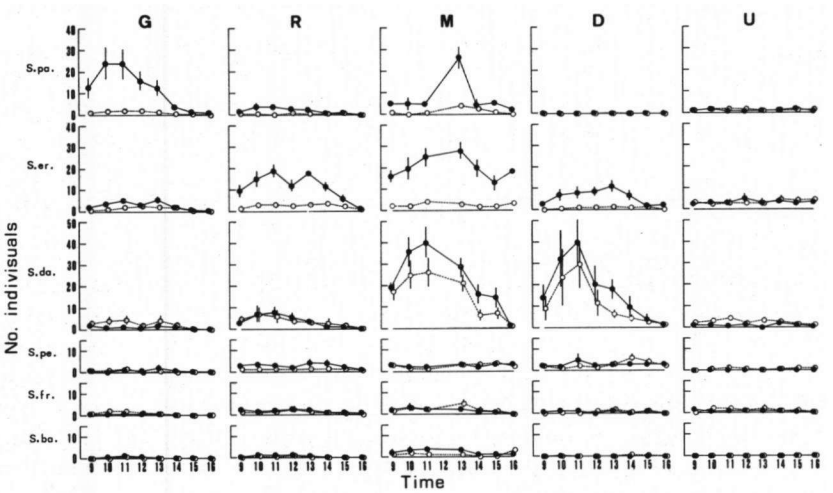

Fig. 2. Diurnal change in the number of Sympetrum individuals. — [S. pa.: *S. parvulum;* — S. er.: *S. eroticum;* — S. da.: *S. darwinianum;* — S. pe.: *S. pedemontanum;* — S. fr.: *S. frequens;* — S. ba.: *S. baccha*].

Tandem counts were used in recording mating activity, because we were not able to accurately observe the number of females ovipositing singly inside the paddy fields. The mature females in all species were generally receptive to conspecific males. The hourly rate of tandems at each site is shown in Figure 3. Tandems occurred in the paddy fields, not in the hills. In the paddy field populations of *S. parvulum, S. eroticum* and *S. darwinianum,* high rates of tandem in the morning always coincided with high flight activity. Such an hourly tandem pattern was also found in the other three species, though they had low densities and did not show any other activity patterns.

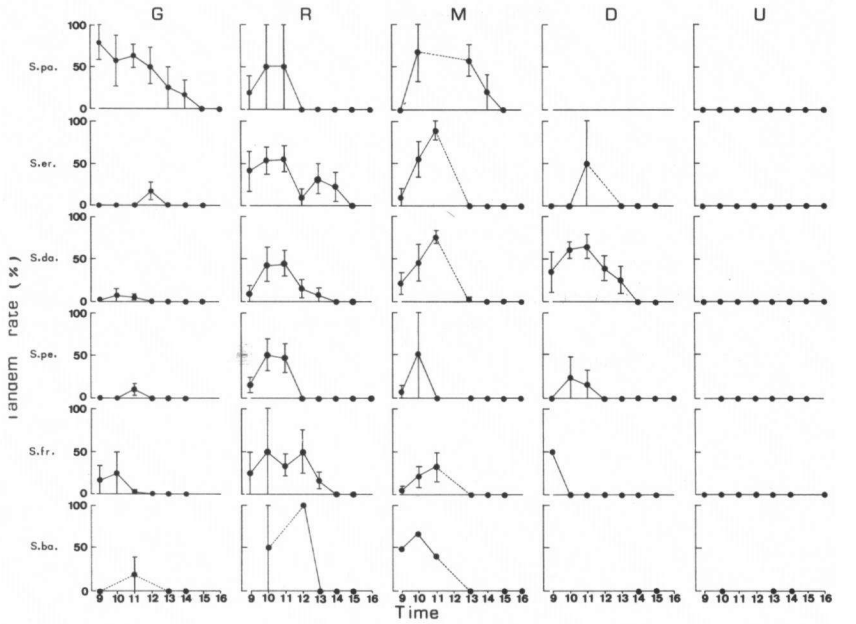

Fig. 3. Diurnal change in the tandem rates (number of tandems/numbers of females). — [For the names of species see Fig. 2.].

Table II shows the hourly population sizes of three species, estimated by JOLLY's (1965) stochastic model. The population size each hour was averaged among sampling days without regard to the standard deviations. Standard errors for the number of sampling days were calculated. Due to low recapture rate, the hourly population sizes of the other four species could not be estimated.

In the paddy fields, the estimated number of males of *S.parvulum* was higher in the morning than in the afternoon in sites G and R. Such a trend was also observed in *S. pedemontanum* in site R. Although standard errors were large, the estimated number of males of *S. eroticum* in all study sites was rather higher around noon than in the morning. In the hills, *S. eroticum* showed the same trend in both sexes.

In the three paddy field species, the estimated male survival rates were higher in the morning than in the afternoon (Tab. III). This suggests that emigration occurred very often in the afternoon. Such movements seem to be in accordance with the evidence on *Sympetrum* diurnal behaviour (TAGUCHI & WATANABE, 1984, 1985, 1986, 1987). In the hills, such a tendency was not observed, suggesting that immigration and emigration occurred constantly throughout the day.

Table II
Estimated number (± SE) of *Sympetrum* individuals at different hours in October, 1981-1984, in five ecologically different study areas — (Numbers of sampling days in brackets)

Species	Sex	Time	G	R	M	D	U
parvulum	♂	09.00	—	—	—	—	—
		10.00	107.2±38.0 (5)	68.2± 8.2 (2)	—	—	—
		11.00	184.1±89.2 (5)	24.0± 12.0 (3)	3.0 (1)	—	—
		12.00	110.1±26.3 (5)	—	—	—	—
		13.00	39.4±13.2 (4)	3.8± 1.5 (4)	87.8± 40.4 (4)	—	1.0 (1)
		14.00	17.8±12.6 (6)	2.7± 0.3 (3)	—	—	—
		15.00	13.5± 7.5 (2)	—	—	—	3.0 (1)
		16.00	—	—	—	—	—
eroticum	♂	09.00	—	—	—	—	—
		10.00	7.0 (1)	87.8± 32.9 (8)	514.8±242.8 (5)	6.0 (1)	5.0 (1)
		11.00	18.6± 5.1 (3)	84.6± 24.0 (11)	487.0±157.8 (5)	8.0 (1)	4.0 (1)
		12.00	20.7± 2.9 (3)	71.3± 17.9 (10)	—	—	13.2±1.4 (2)
		13.00	12.7± 4.4 (5)	169.7± 99.7 (12)	275.1± 93.8 (9)	7.0±4.0 (3)	11.0±1.0 (2)
		14.00	5.6± 1.6 (4)	116.5± 62.8 (6)	135.1±114.9 (4)	5.5±2.5 (2)	13.5±1.5 (2)
		15.00	7.0 (1)	10.0± 2.6 (3)	341.2 (1)	—	4.3±0.9 (3)
		16.00	—	—	—	—	—
	♀	09.00	—	—	—	—	—
		10.00	3.0 (1)	—	—	—	8.0 (1)
		11.00	4.0 (1)	—	—	—	8.2±5.2 (2)
		12.00	3.0 (1)	7.0 (1)	—	—	13.3±4.3 (2)
		13.00	—	4.0 (1)	3.0 (1)	—	11.1±2.1 (2)
		14.00	2.0 (1)	9.0± 8.0 (2)	—	—	10.0±1.0 (2)
		15.00	3.0 (1)	2.0± 0.0 (2)	—	—	13.1 (1)
		16.00	—	—	—	—	—
pedemontanum	♂	09.00	—	—	—	—	—
		10.00	—	565.1±551.7 (4)	1.0 (1)	5.0 (1)	—
		11.00	—	56.3± 39.2 (4)	—	36.0 (1)	—
		12.00	—	70.0± 10.0 (2)	—	—	—
		13.00	—	38.6± 13.0 (3)	3.5± 1.5 (2)	5.0 (1)	—
		14.00	—	27.4± 15.0 (6)	—	—	—
		15.00	—	7.0 6 (1)	—	3.0 (1)	—
		16.00	—	—	—	—	—

Estimated daily survival rate by Jolly's model was also averaged (Tab. IV), assuming a constant rate of survival throughout October among the sites. Since it is unlikely that most individuals perished during the study period, the daily survival rate was regarded as a daily emigration rate. No individual of *S. frequens* and *S. infuscatum* was recaptured over weeks.

The life expectancy (L) in each sex and species was calculated by the equation $L=1/(1-S)$, where S is the daily survival rate. Since S is also understood as the daily emigration rate, the life expectancy was regarded as residentiality. In *S. eroticum* it was the longest (38.0 days in males and 8.3 days in females), while in female *S. darwinianum* it was the shortest (3.6 days). Since October is the closing season of *S. pedemontanum* (TAGUCHI & WATANABE, 1984), the relatively short residentiality values for both sexes appear reasonable. *S. darwinianum* and *S. baccha* also had relatively short residentiality. This may be due to high migration rate. On the other hand, relatively long male and female residentiality

Table III

Estimated survival (emigration) rates (± SE) of *Sympetrum* individuals at different hours in October, 1981-1984, in five ecologically different study areas — (Number of sampling days in brackets)

Species	Sex	Time	G	R	M	D	U
parvulum	♂	09.00	1.068±0.161 (5)	0.891±0.177 (2)	—	—	—
		10.00	1.019±0.142 (5)	1.246±0.477 (3)	—	—	—
		11.00	1.161±0.298 (5)	—	0.212±0.212 (2)	—	—
		12.00	0.998±0.350 (4)	0.000±0.000 (4)	—	—	—
		13.00	0.346±0.269 (6)	0.092±0.065 (5)	—	—	—
		14.00	0.583±0.583 (2)	0.000 (1)	—	—	0.667 (1)
		15.00	—	—	—	—	—
		16.00	—	—	—	—	—
eroticum	♂	09.00	0.600 (1)	0.867±0.089 (8)	1.350±0.338 (6)	0.200 (1)	1.000 (1)
		10.00	0.792±0.051 (3)	1.073±0.183 (11)	0.884±0.093 (9)	0.333 (1)	0.800 (1)
		11.00	0.660±0.313 (4)	0.874±0.149 (11)	0.901±0.206 (4)	—	0.608±0.517 (2)
		12.00	0.750±0.214 (4)	0.677±0.220 (12)	—	0.083±0.083 (3)	0.133±0.000 (2)
		13.00	0.100±0.042 (5)	0.354±0.126 (8)	0.212±0.169 (4)	0.067±0.067 (2)	1.000 (1)
		14.00	0.300±0.300 (3)	0.050±0.028 (3)	0.001 (1)	—	0.139±0.073 (3)
		15.00	—	—	—	—	—
		16.00	—	—	—	—	—
	♀	09.00	0.333 (1)	—	—	—	0.714 (1)
		10.00	1.000 (1)	—	—	—	0.333±0.333 (2)
		11.00	0.250 (1)	0.182 (1)	—	—	1.123±0.043 (2)
		12.00	0.000 (1)	0.500±0.500 (2)	— —	0.408±0.008 (2)	
		13.00	0.333 (1)	0.400 (1)	—	—	0.886±0.314 (2)
		14.00	0.250 (1)	2.000 (1)	—	—	0.682 (1)
		15.00	—	—	—	—	—
		16.00	—	—	—	—	—
pedemontanum	♂	09.00	—	2.035±1.384 (4)	0.250 (1)	0.500 (1)	—
		10.00	—	0.726±0.490 (4)	0.000 (1)	1.500 (1)	—
		11.00	—	0.610±0.060 (3)	—	—	—
		12.00	—	1.317±0.726 (3)	—	0.000 (1)	—
		13.00	—	0.387±0.129 (6)	—	—	—
		14.00	—	0.333 (1)	—	0.000 (1)	—
		15.00	—	—	—	—	—
		16.00	—	—	—	—	—

in *S. parvulum* was expected on the basis of the population age structure in this species, where, due to the emergence pattern, the individuals occurring in October are of different ages (cf. TAGUCHI & WATANABE, 1984).

INDIVIDUAL MIGRATION BETWEEN STUDY SITES

The recorded average distances of flight are shown in Table V. Since the number of sites surveyed and the number of days sampled were different each year, the mean distance of flight was not compared between years. The 1982 data were also discarded because most sampling days were dull, with low activity of movements.

S. parvulum and *S. eroticum* covered relatively short distances (ca. 250 m/day, which is similar to the distance between sites G and R). Indeed, about 40% and

Table IV

Mean (± SE) daily survival rate (S) and the mean duration of residentiality (L, in days) in *Sympetrum* — (Number of sampling dates in brackets)

Species	Males			Females		
	n	S	L	n	S	L
parvulum	12	0.870±0.043	7.7	3	0.829±0.090	5.9
eroticum	16	0.974±0.079	38.0	7	0.879±0.090	8.3
darwinianum	7	0.828±0.067	5.8	2	0.719±0.292	3.6
pedemontanum	7	0.805±0.068	5.1	5	0.721±0.053	3.6
frequens	—	—	—	—	—	—
baccha	4	0.763±0.058	4.2	1	0.731	3.7
infuscatum	—	—	—	—	—	—

Table V

Mean (± SE) flight distance (m/day) of *Sympetrum* within an October day — (n = number of individuals recaptured)

Species		1981		1983		1984	
		n	m/day	n	m/day	n	m/day
parvulum	♂	19	299±103	24	446±117	23	250± 61
	♀	1	292	1	243	3	116± 32
eroticum	♂	17	238±130	10	221± 63	30	250± 71
	♀	7	297±204	4	195± 90	8	496±154
darwinianum	♂	9	569±225	4	380±169	0	—
	♀	4	1057±819	1	172	0	—
pedemontanum	♂	16	605±189	0	—	2	278±209
	♀	3	318±207	3	568±552	4	397±100
frequens	♂	0	—	0	—	0	—
	♀	0	—	0	—	1	4560
baccha	♂	4	498±323	2	821± 91	0	—
	♀	1	88	0	—	1	688
infuscatum	♂	0	—	0	—	0	—
	♀	0	—	0	—	0	—

30% respectively of recaptured males of the two species occurred within sites G and R (Tab. VI). Although the data from the sites D and U were gathered during two years, the low recapture rate of *S. darwinianum* and *S. baccha* and the fact that they were recaptured in all the study sites, irrespectively of the natural barriers such as forests, suggests that they fly further than other species, though they do show a preference for particular habitats, peculiar by their topography and vegetation.

Table VI

Recapture rate (% ± SE) of *Sympetrum* individuals within five ecologically different study areas on various sampling days in October, 1981-1984 — (n = number of years)

Species	Sex	G		M				U	
		n	%	n	%	n	%	n	%	n	%
parvulum	♂	3	39.4±10.0	4	7.5±3.4	4	13.2±5.1	2	0.0± 0.0	2	12.0± 1.3
	♀	3	9.2± 1.0	4	3.9±3.9	4	4.0±2.9	2	0.0± 0.0	2	10.3± 4.7
eroticum	♂	3	27.7± 8.9	4	22.7±7.5	4	15.8±3.5	2	9.9± 5.0	2	9.4± 5.0
	♀	3	3.4± 3.4	4	4.4±3.2	4	4.5±0.6	2	47.2±47.2	2	16.0±11.1
darwinianum	♂	3	0.0± 0.0	4	1.0±0.6	4	2.2±0.8	2	1.6± 0.9	2	0.0± 0.0
	♀	3	0.0± 0.0	4	0.1±0.1	4	3.3±1.9	2	0.5± 0.5	2	0.0± 0.0
pedemontanum	♂	3	2.9± 2.9	4	18.6±8.0	4	5.5±2.6	2	7.8± 1.1	2	0.0± 0.0
	♀	3	0.0± 0.0	4	7.5±5.4	4	3.6±2.0	2	8.6± 0.3	2	0.0± 0.0
frequens	♂	3	0.0± 0.0	4	0.0±0.0	4	0.0±0.0	2	0.0± 0.0	2	0.0± 0.0
	♀	3	0.0± 0.0	4	0.0±0.0	4	0.0±0.0	2	0.0± 0.0	2	0.0± 0.0
baccha	♂	3	16.7±16.7	4	3.3±1.9	4	5.5±2.4	2	0.0± 0.0	2	0.0± 0.0
	♀	3	0.0± 0.0	4	6.3±6.3	4	1.6±1.6	2	0.0± 0.0	2	0.0± 0.0
infuscatum	♂	3	0.0± 0.0	4	0.0±0.0	4	0.0±0.0	2	0.0± 0.0	2	0.0± 0.0
	♀	3	0.0± 0.0	4	0.0±0.0	4	0.0±0.0	2	0.0± 0.0	2	0.0± 0.0

DISCUSSION

Sympetrum investigations in the paddy fields have revealed a variety of community structures. *S. parvulum* showed very tight population structure in site G, occurring in clearly delimited demographic units with little exchange of individuals. Another clear example of this is also the tiny, *Nannophya pygmaea* (FUJITA et al., 1978). *Cordulia aenea* also seem to be restricted to the same pond throughout their life span, though little information on their maiden flight habitats is known (UBUKATA, 1981). *S. frequens* and *S. darwinianum* had a loose population structure, being virtually ubiquitous over wide areas. The community structure also became loose in the paddy fields where they were dominant.

All of the *Sympetrum* species studied in our paddy fields are summer species (sensu CORBET, 1962). However, the emergence dates and patterns are different in each species: *S. pedemontanum* were the first to emerge while *S. parvulum* continued to emerge till late-September (cf. TAGUCHI & WATANABE, 1984). MICHIELS & DHONDT (1987) suggested that sexual maturation in *S. pedemontanum* is reached earlier than in any other *Sympetrum* species. Therefore, the *Sympetrum* community of the paddy fields in October consists of species and individuals of diverse age.

Observations on variation in the extent of the shaded areas within a day or

throughout a season indicate that the flying habits of some species, such as *S. eroticum* (cf. TAGUCHI & WATANABE, 1987), clearly depend upon the sunlit area of paddy fields. Most of them preferred the sunlit area throughout the day in October. However, few of them behaved aggressively in the sunlit area of paddy fields, though MICHIELS & DHONDT (1987) did report interactions between *Sympetrum* species in Belgium. Indeed, we did not notice inter- or intraspecific territorial conflicts during October, save for *S. parvulum,* as recorded also by UEDA (1979). Some interference between *Sympetrum* species had also been evidenced by MOORE (1964).

It is generally assumed that many dragonfly species are reproductively active only during a part of the day (e.g. JACOBS, 1955; MOORE, 1953; MILLER, 1982). In the paddy fields, all *Sympetrum* were active in the morning. KINOSHITA & OBI (1931) reported that *S. frequens* oviposited during 8:00-12:00 h. Mature individuals of *S. risi* also visited bogs in the October mornings (ARAI, 1983). Although UEDA (1979) stated that territorial behaviour of *S. parvulum* was performed around noon, most individuals copulated and oviposited in the morning. However, in October interspecific temporal partitioning did not occur in sympatric species of similar sizes, as suggested also by TAGUCHI & WATANABE (1985, 1986, 1987). MOORE (1957) stated that where species of different sizes occur in the same area interspecific interaction causes proportionately more members of the smaller species to disperse.

RUDOLPH (1978) emphasised that a more diversified dragonfly fauna is to be found at less polluted permanent pools with great productivity, i.e. dense vegetation and rich arthropod fauna as a food supply. Most larvae of coexisting species (*Tetragoneuria cynosura, Celithemis elisa, C. fasciata* and *S. vicinum*) consumed medium-sized cladocerans, ostracods, oligochaetes, etc., as reported by MERRILL & JOHNSON (1984). Even at lower densities they may play an important trophic role as primary and secondary carnivores (BENKE et al., 1982; CROWLEY et al., 1987). On the other hand, the adult *Sympetrum* preyed upon small Hymenoptera, Lepidoptera, Diptera or Hemiptera, while they were preyed upon by large dragonflies, spiders or birds (cf. also JACOBS, 1955; CORBET, 1962; RAM & PRASAD, 1978; TAGUCHI & WATANABE, 1985, 1987). Small Diptera and Lepidoptera appear the most available prey for *Aeshna affinis* in the evening (UTZERI & RAFFI, 1983). In the paddy fields, no difference in *Sympetrum* prey preference has been reported, nor is any local variation in the community structure of prey insects known. Although some insects, such as the veliid bug *Microvelia douglasi atrolineata,* are considered to be the most important natural enemies of the brown planthopper *Nilaparvata lugens* in paddy fields (NAKASUJI & DYCK, 1984), no *Sympetrum* has yet been assessed as a predator of pest insects. Since each of the paddy fields studied could provide abundant *Sympetrum* food, the habitats chosen would not depend upon prey communities. However, the *Sympetrum* community in each paddy field was

peculiar in terms of the dominant species. This would suggest that the habitat preference is not conditioned by the foraging habits.

In the hills, the community structure of prey insects was generally different from that in the paddy fields. HIGASHI (1973) observed feeding behaviour of *S. frequens* in the coniferous forests, where there was an excess of females. Since no mating took place in the hills, such places may serve as a feeding area, and presumably also provide roosting sites. TAGUCHI & WATANABE (1987) suggested that the hills with deciduous forests represent a nursing area during the maturation of *S. eroticum*, from July to August. WATANABE (1986) also showed that the hills near paddy fields serve as a nursing area for *Orthetrum japonicum*. Therefore we tentatively assume that, save for the case of *S. pedemontanum*, the hills might be regarded as a *Sympetrum* nursing area.

S. darwinianum also roosted in site G. Considered the topographic feature of the site, the roosting area might be mainly confined to the shaded portions of the habitat. WATSON et al., (1982) showed that the diversity of dragonfly fauna gives an indication of water quality. However, the community structure of *Sympetrum* in a paddy field in October seems to depend upon the habitat preference, influenced by the topographic feature of the paddy fields.

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