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PATTERNS OF DISTRIBUTION AND TERRITORIALITY IN THE TWO MALE FORMS OF *MNAIS PRUINOSA PRUINOSA* SELYS (ZYGOPTERA: CALOPTERYGIDAE)*

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In the study area 2 forms of *M. p. pruinosa* males (f. *esakii* and f. *strigata*) occurred. Immature damselflies dispersed away from the stream. After maturation they returned to the stream and often moved along the stream searching for territory sites. Once *esakii* males established their territories, *strigata* males stettled around these territories as satellites. The males of *esakii* had many mating chances, utilizing their territories. Male movements and settlement were influenced by fighting among the males and also by the frequency of female appearances. Both *esakii* and *strigata* males aggregated in the habitat sections where many females appeared. Mating strategies of *esakii* and *strigata* males are described as territorial-guarding and satellite-multicopulation (nonguarding), respectively. A possible mechanism for coexistence of both types of males is suggested.

INTRODUCTION

Mate competition occurs both before and after copulation (CADE, 1979). In *M.p. pruinosa* precopulatory mating competition occurred as in territoriality, i.e. *esakii* males established territories in suitable habitat, while *strigata* males were nonterritorial and stayed around the territories of *esakii* (HIGASHI, 1976, 1981). NOMAKUCHI et al. (1984) concluded that this dominance relation represented territorial and satellite or sneaking mating strategies by *esakii* and *strigata*, respectively (ALCOCK, 1982; KREBS & DAVIES, 1981).

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Postcopulatory sperm competition in dragonflies is reported by several investigators (e.g. WAAGE, 1979, 1982; MILLER & MILLER, 1981, 1982; FINCKE, 1984; McVEY & SMITTLE, 1984). In *M.p. pruinosa*, the behavioural aspects of postcopulatory competition were recognized as noncontact strategy *(esakii)* and multicopulation strategy (nonguarding, *strigata*) (NOMAKUCHI et al., 1984). It is interesting that nonguarding *strigata* males remain in the population, since it is expected that females mating with *strigata* males lay few eggs fertilized by these males before remating with *esakii* males.

To consider reproductive success of dragonflies it is important to know the ratio of territorial males to total males and the distribution of males on the stream. This is because the reproductive success of a male is often influenced by other males' behaviour and their abundance. In this study, we will show the movement and distribution of mature males along the stream, and discuss the possible mechanism of coexistence of both forms of males.

STUDY AREA AND METHODS

This study was performed at upper reaches of the Ino River (cf. HIGASHI, 1976, 1981; HIGASHI et al., 1979). The stream was divided longitudinally into 45 habitat sections of 10 m length each. The field censuses were made in early summers of 1977, 1978, 1982 and 1983.

The damselflies were captured by insect net along the stream and forest road and individually marked on the wings by fast-drying ink. The marked individuals were released after recording the degree of maturation and the habitat section they were captured in. The degree of maturation was classified into four stages M0, M1, M2, and MA (HIGASHI et al., 1982). The date and habitat section of all the subsequent recoveries were recorded for each individual. Iterations of the procedure were made for unmarked individuals on each day during the flying season. The frequencies of fighting and mating behaviour were recorded in the central 12 habitat sections during the season of 1983.

RESULTS

SEASONAL CHANGES IN THE NUMBER OF INDIVIDUALS

The emergence of this species began in late April (HIGASHI, 1976, 1981). After emergence the individuals dispersed from the stream, and they fed on small insects in sunlit areas, such as a forest road along the stream (HIGASHI et al., 1982). After maturation they returned to the stream.

The seasonal changes in the number of individuals observed on this stream are shown in Figure 1. Their density reached a peak in early May and their flying season ended in late June. The decrease in number of individuals in late April was caused by cloudiness. *Mnais p. pruinosa* is apparently a "spring type" species (CORBET, 1954) based on this pattern of seasonal changes in the number. The number of *esakii* males was larger than that of *strigata* throughout their flying season (Fig. 1a).

The number of females observed on the stream is also shown in Figure 1b.

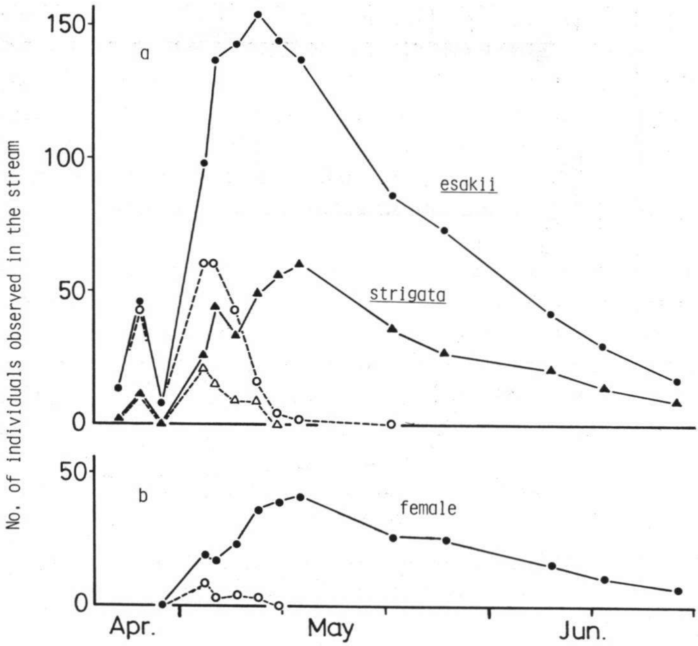

Fig. 1. Seasonal changes in the number of *Mnais p. pruinosa* observed on the stream (in 1982). Broken and solid lines indicate respectively immature and mature individuals.

Mature females usually spent most of the daytime in surrounding areas of the stream (e.g. forest and forest road) and sometimes came down into the stream for mating and oviposition (HIGASHI, 1976, 1981). Consequently only small numbers were observed on the stream.

THE HEIGHT OF PERCH SITES IN *ESAKII* AND *STRIGATA* MALES

Mature males of *esakii* established territories, including oviposition sites, on the stream, while *strigata* males were nonterritorial and stayed arround the territories of *esakii* males (HIGASHI, 1976, 1981; NOMAKUCHI et al., 1984). Therefore, *esakii* males perched on the stones near the water surface, while *strigata* males perched on the vegetation growing along the stream. The height of perch sites above the water surface was estimated by eye for each male. The results are shown season-wise in Figure 2. This figure indicates that *esakii* and *strigata* males perch at similar heights early in the season (pre-reproductive and transitional periods). The pre-reproductive and reproductive periods are defined by CORBET (1962), and "transitional period" is used here as during the period there are mature and immature individuals in the population. After 13 May

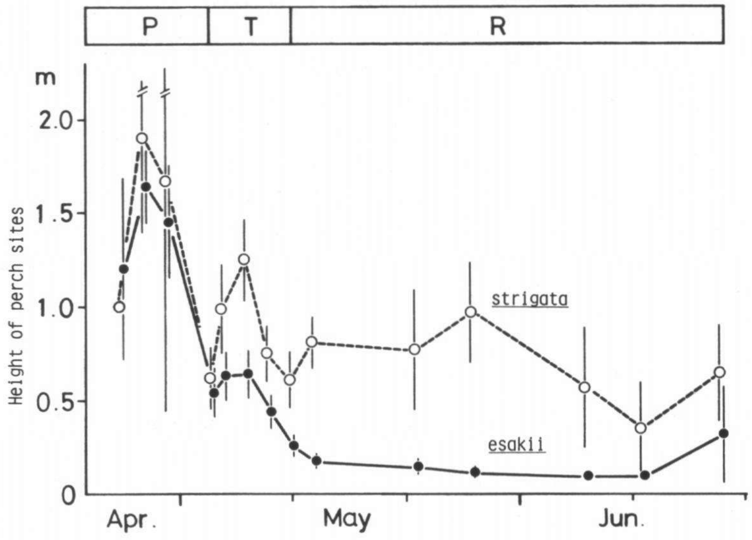

Fig. 2. Seasonal changes in the height of males' perch sites above the water surface (in 1982). Vertical line indicates standard error. P, T and R represent pre-reproductive, transitional and reproductive periods, respectively.

(reproductive period) *esakii* males established their territory and perched on stones or plants at a height of ca 10 cm, while *strigata* males were nonterritorial and perched on the vegetation at a height of ca. 60 cm.

THE MOVEMENT OF MALES ALONG THE STREAM

Male movements along the stream were studied in the transitional period (May 4-13) and in the reproductive periods (May 11-22, May 22-June 6). In calculating

Table I

Comparison of male movements between transitional and reproductive periods (in 1982)

Male forms	May 4-13		May 11-22		May 22 -Jun 6
esakii	7.6±9.2 (n=57)	— ** —	3.3±7.5 (n=66)	— n.s. —	1.7±3.1 (n=30)
strigata	5.3±9.7 (n=15)	— * —	0.5±0.9 (n=16)	— n.s. —	1.4±2.1 (n=7)

Distances of male movements during the transitional period (from 4 to 13 May), and during the reproductive periods (from 11 to 22 May and from 22 May to 6 June) are shown as mean values with standard deviations (in meter per day). — U-test of Mann-Whitney is used to test the difference between these periods. — n: No. of males. — *: $p < 5\%$. — **: $p < 1\%$. — n.s.: non significant.

the mean distance, males which were discovered more than two times in the given period were used and the mean distance of their movements per day is shown in Table I. It can be seen that this distance decreases from the transitional period to the reproductive period, i.e. males moved frequently in the transitional period, less so in the reproductive period. Moreover, 55.5% of the above males were observed in the same habitat section in the reproductive period and there were 26.4% in the transitional period. It is suggested, from these results, that most *esakii* males have settled in a particular area as territory holders in the reproductive period and that most *strigata* males also have settled as satellites in the same period.

FIGHTING FREQUENCY AMONG THE MALES

From the above results it is expected that fighting among males, which occurred in establishing or defending their territories, would decrease during the transitional period. Consequently the frequence of fighting was observed in the transitional (May 2-10) and reproductive (May 12-23) periods in 1983. Field censuses were made 15 times in the transitional period, and 11 times in the reproductive period. The fighting frequency and number of males observed during the census are shown in Table II.

Table II

Frequency of fighting behaviours observed among the males during the transitional and reproductive periods (in 1983)

Combinations of male forms		May 2-10 (n=15)	May 12-23 (n=11)	U-test
esakii — *strigata*		3.53±2.78	1.36±1.43	*
esakii — *strigata*		1.45±1.50	1.73±2.38	n.s.
strigata — *strigata*		0.33±0.47	0.45±0.66	n.s.
Average No. of males	*esakii*	34.1 ±8.9	31.5 ±5.5	n.s.
	strigata	8.5 ±3.6	8.6 ±2.1	n.s.

n: No. of census. — Frequency of fighting behaviours is shown as the frequency per census (100 m length along the stream). — U-test of Mann-Whitney is used to test the difference between 2-10 May and 12-23 May. — *: significant ($p < 5\%$) n.s.: non significant.

The average density of males was almost the same during the two periods. The frequency of clashes among the *esakii* males is higher in the transitional period than in the reproductive period (significant, $p < 5\%$ by U-test of Mann-Whitney), while the frequencies of fighting between *esakii* and *strigata* males, and among *strigata* males do not differ significantly. This suggests that the fighting among *esakii* males results in their dispersal from high to low density sections in the transitional period), and that the frequency of fighting decreases after settlement of males into established territories (in the reproductive period).

SETTLEMENT AND MATING CHANCE

Habitat utilization was studied by recording the mature males who appeared in each habitat section on 11 and 22 May (Fig. 3). These days were chosen as representative of the reproductive period in Figure 2. It can be seen that male habitat utilization varies among habitat sections. This suggests that males prefer some habitat sections over others.

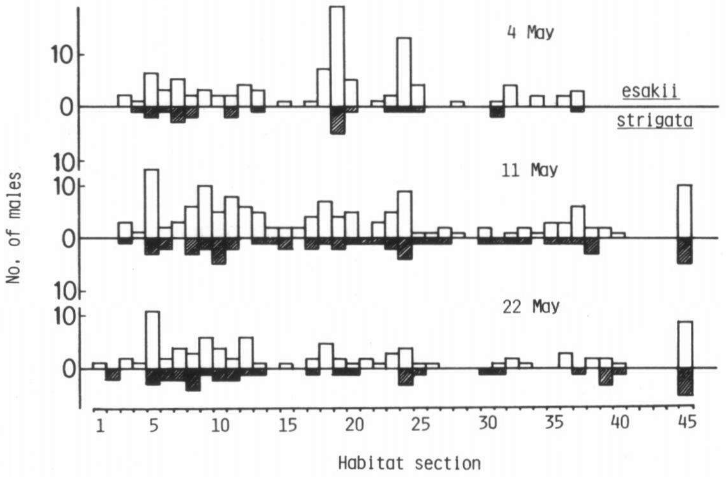

Fig. 3. The distribution of two forms of male along the stream during the reproductive period (11, 22 May, 1982).

Mature males and females were frequently observed at the habitat sections where the oviposition sites were abundant. Therefore, to detect the utilization of each habitat section by both sexes, the numbers of individuals observed during census (15 times) in the reproductive period are summed in each of 41 habitat sections. Kendall's rank correlation coefficients of total number in each habitat section were calculated between *esakii* males and females, and between *strigata* males and females, respectively (Fig. 4). The values were 0.51 and 0.33, respectively and these values are significant ($p < 0.1\%$ and $p < 1\%$). Kendall's rank correlation coefficient between *esakii* and *strigata* males is 0.65 (significant, $p < 0.1\%$), and this is in agreement with the observations of HIGASHI (1981). Both forms of males utilize and settle at the habitat section where females frequently appear for oviposition.

To compare the mating chance of males among 11 habitat sections, the correlation between the mating frequency of males and the number of female appearances in each habitat section was examined (Fig. 5). Kendall's rank correlation coefficients are significant for *esakii* ($p < 5\%$) and *strigata* ($p < 1\%$). This suggests that the males settle at the habitat section where they are able to mate frequently. This figure shows also that the mating frequency of *strigata* males is not lower than that of *esakii* males in each habitat section. Exceptionally, in habitat section No. 24 (the points most to the right), were most females appeared, the mating frequency of *strigata* males was higher than that of *esakii* males. Since the density of *esakii* males is very high in this section, loss of mating chance by male interference may occur in *esakii* males.

The reproductive success of both forms of males is quite dependent on the oviposition behaviour of the females, namely, whether or not they copulate again with other males before they oviposit (NOMAKUCHI et al., 1984). Table III shows the record of ovipositions observed during the population census. It seems that oviposition categories (a) & (b) and (c) & (d) are advantageous to *esakii* and *strigata,* respectively. The frequency of oviposition categories (a) & (b) is larger than that of (c) & (d). This suggests that the probability for females to be fertilised by *esakii* males is 83.6%, by *strigata* males 16.4%. It is considered, therefore, that the oviposition conditions in the study area are advantageous to *esakii* males.

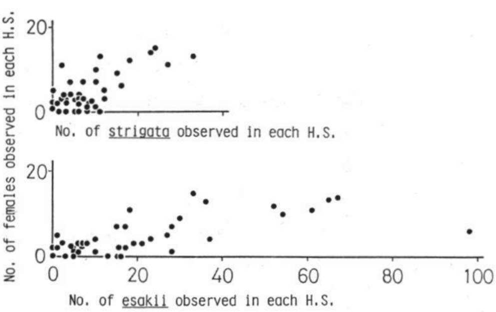

Fig. 4. Correlation between the males and females appearing in each habitat section (H.S.) in 1977.

DISCUSSION

TERRITORY ESTABLISHMENT AND MOVEMENT OF THE MALES ALONG THE STREAM

The immature damselflies disperse away from the water and their dispersion may be affected by circumstances such as e.g. vegetation around the water (e.g. PAJUNEN, 1962; PARR, 1973, 1976; CORBET, 1980). This phenomenon was recognized in the present study. After maturation the males synchronously returned to the stream, and aggregated in the sunny area of the stream. In the transitional period, *esakii* males seem to compete with their rivals for territory site. Fighting among *esakii* males occurred frequently in this period. As a result, the male which could not set up a territory seems to move and search for another site. Thus, fighting among *esakii* males is considered to influence their movement

Table III
The number of ovipositions observed during the population census

Years	No. of ovipositions	Oviposition category					
		(a)	(b)	(c)	(d)	(a)&*(b)*	*(c)*&*(d)*
1977	44	33	6	3	2	39	5
1978	29	14	8	0	7	22	7
Total	73	47	14	3	9	61	12
%	*100*					*83.6*	*16.4*

(a) Oviposition guarded by territorial *esakii;* — (b) Oviposition near the territorial *esakii;* — (c) Oviposition near the nonterritorial *strigata;* (d) Solitary oviposition

(MOORE, 1964; HIGASHI, 1969). Also *strigata* males moved along the stream in the transitional period. They seem to search for a satellite area. Once *esakii* males found and established their territories and *strigata* males settled around the territory, they likely did not move.

In *Hetaerina americana,* most females appeared in certain areas and in these areas the highest number of males was observed (JOHNSON, 1962). In *M.p. pruinosa,* both *esakii* and *strigata* males were observed to aggregate and to settle at the habitat section where many females appeared and they are able to mate frequently (Fig. 4).

In this study, it was noticed that the mating chance of males varied among the habitat sections (Fig. 5). Apparently some males could settle at a suitable habitat section (many females appeared there), while others were forced to settle at an unsuitable one (few females appeared there).

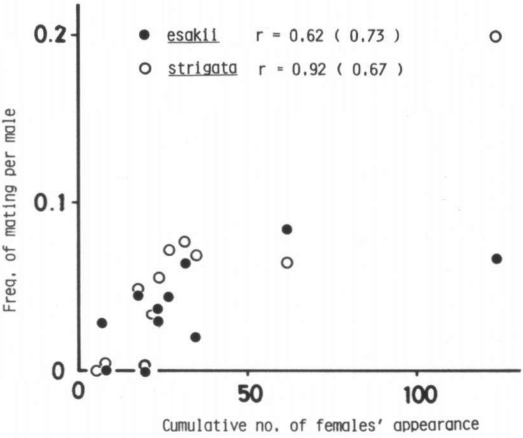

Fig. 5. Correlation between the frequency of mating and the number of female appearances in each habitat section (in 1983). — Black circles and white circles indicate *esakii* and *strigata* males, respectively.

COEXISTENCE OF *ESAKII* AND *STRIGATA* MALES IN THE POPULATION

The reproductive success of the males is defined as the product resulting from multiplying the number of copulations by the fertilization rate per copulation (WAAGE, 1979a, 1979b; FINCKE, 1984). The frequency of copulations in suitable territory in the Ino River is almost equal for *esakii* and *strigata* males (Fig. 6; NOMAKUCHI et al., 1984). However, the insemination rate of *strigata* males is considered to be relatively low, because most females mated by *strigata* do not oviposit without mating again and thus (assuming sperm displacement) they have fewer fertilizations.

In *M.p. pruinosa,* it is not known why *strigata* males do not occupy territories and how they can coexist with the *esakii* males in this area. Figure 6 showing the schema of hypothetical reproductive success for both forms of males on the Ino River, offers a possible explanation. Territory quality is expressed as the frequency of female appearances, and these curves are shown arbitrarily as monotonously decreasing functions. Curve E indicates the reproductive success of territorial *esakii* males, and is higher than the curves S1 and S2, which represent the reproductive success of *strigata* males, because the fertilization rate of *strigata* males is considered to be lower than that of *esakii* males, as described above. If the reproductive success of *strigata* males is S1, their offspring can join in this population, and if the curve is S2, only *esakii* males exist in this population.

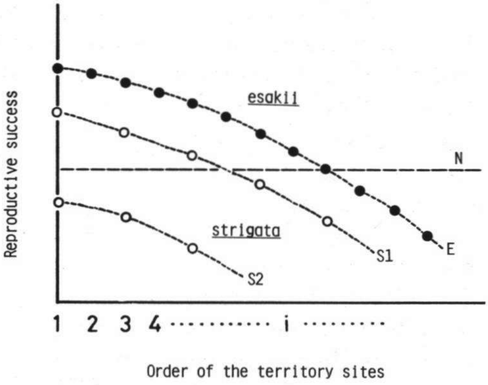

Fig. 6. Hypothetical schema showing the reproductive success of both forms of males. The curve E represents the reproductive success of territorial *esakii*. The curves S1 and S2 represent the reproductive success of nonterritorial *strigata*. The line N indicates the threshold of reproductive success.

Whether or not the reproductive success of *strigata* belongs to curve S1 seems to be dependent on several factors: (1) the frequency of females' solitary oviposition and (2) the degree of sperm displacement during copulation (FINCKE, 1984; WAAGE, 1979a, 1979b).

The sexual selection and evolutionarily stable strategy (ESS) theory provides valuable insight into the evolution and dynamics of insect behaviour (WAAGE, 1983). Waage adapted this theory to the behaviour of *Calopteryx maculata* and documented the male/female interactions and territorial contests. If the behaviours of two forms of males in this population are ESS, the mating success per *esakii* male should be equal to that of a *strigata* male. Then the ratio of mating success between *esakii* and *strigata* males should coincide with the ratio between their densities. In this study, mating frequency is not different between them and the opportunity of fertilization are 83.6% *(esakii)* and 16.4% *(strigata)*, respectively (Tab. III). However, the ratio of marked males between *esakii* and *strigata* was 61,4(%):38.5(%) in 1982. Other factors, such as the degree of sperm displacement and survivorship of the larvae, may influence the difference between the opportunity of fertilization and the ratio of adult densities.

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