Male reproductive polymorphism and form-specific habitat utilization of the damselfly *Mnais pruinosa* (Zygoptera: Calopterygidae)

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Habitat utilization patterns were studied in damselfly males, *Mnais pruinosa*, which have two male forms with different reproductive behaviors. The '*esakii*' (orange-winged males) were territorial around oviposition sites, while the '*strigata*' (hyaline-winged males) were non-territorial, often sneaking into the *esakii's* territory or loitering on the foliage of vegetation along stream banks. The place in the stream in the study area where females frequently appeared was covered by reeds and had abundant oviposition sites. It was difficult for the territorial *esakii* to stay there because the crowded reeds prevented them from defending their territory and discovering the females. Furthermore, there was competition for the limited territorial space with another species, *Mnais nawai*. *Strigata* males concentrated in this place in direct proportion to the number of females. Females frequently mated with *strigata* males and probably deposited eggs fertilized by *strigata* sperm rather than *esakii* sperm. The density of *strigata* was higher than that of *esakii* in this study area. If the average reproductive success of *esakii* and *strigata* males is equal, this may indicate that the equilibrious point between the two male forms is biased toward *strigata*.

Key words: damselfly; habitat utilization; male polymorphism; mating system; territory.

INTRODUCTION

Intraspecific variations of behavior and morphology have attracted attention recently in many animals (see Krebs & Davies 1991). This attention has focused on the evolutionary maintenance mechanisms of these variations. Maynard Smith (1976) demonstrated mathematically that few strategies could coexist in the same population in a frequency-dependent manner, known as mixed evolutionary stable strategies (mixed ESS). However the concept of 'mixed ESS' has been rethought recently, as Dominey (1984) pointed out that 'mixed ESS' should be applied only to stochastic strategies and not to polymorphism. Although genuine mixed ESS may be rare in nature (Dunbar 1982), a genetic polymorphism in a frequency-dependent equilibrium has been found often (Clarke & Partridge 1987). Polymorphism in reproductive characters (morphology and behavior) has especially interested researchers, and much field work has been carried out with birds

(van Rhijin 1973), fish (Gross 1984; Maekawa & Onozato 1986; Houde 1988) and insects (Grant *et al.* 1974; Hamilton 1979; Robertson 1985). However only a small amount of this field work shows that the equilibrious proportion of polymorphism is variable according to environmental change or habitat heterogeneity (Hagen & Moodie 1979; Hagen *et al.* 1980; Endler 1991).

In the damselfly *Mnais pruinosa*, a population of the two male forms *esakii* (orange-winged males) and *strigata* (hyaline-winged males) was seen near Fukuoka City, Japan (Nomakuchi *et al.* 1984). The former was territorial and the latter was non-territorial (Nomakuchi *et al.* 1984). The sympatric existence of both male forms was attributed to the balance of their reproductive success (Nomakuchi & Higashi 1985). Furthermore, in the preceding studies, the ratio of the number of *esakii* and *strigata* was usually biased toward *esakii* males, as conditions were favorable to them. As the *esakii* males occupied most of the oviposition sites, which were distributed patchily throughout the stream, the majority of females copulated with *esakii* males and oviposited with

their guarding. Assuming male reproductive success was equal between the male forms, it would appear that there was a proportional bias toward the *esakii* form. However the author found a local population in which the ratio of *esakii* males to *strigata* males was low. This paper clarifies the conditions that have influenced the ratio between the two forms, and discusses the mechanism of the change in the form ratio.

STUDY AREA AND METHODS

The study area was located at the upper stream of the Muromi River in Fukuoka City, Japan

(Fig. 1a). In order to determine the distribution of damselflies throughout this river, field investigations of both adult density and environmental characteristics were performed at 12 areas marked throughout the river from 18 May to 12 June in 1980, and three areas marked from 12 May to 4 June in 1981. The stream-length investigated at each area was 80–200 m. Damselflies were captured with an insect net and released after marking. The number of damselflies was counted every 10 m in an area and the mean number calculated for each area.

U1, one of the study areas, was chosen for a detailed population study in 1980 and 1981. It was divided into four segments (A, B, C and D),
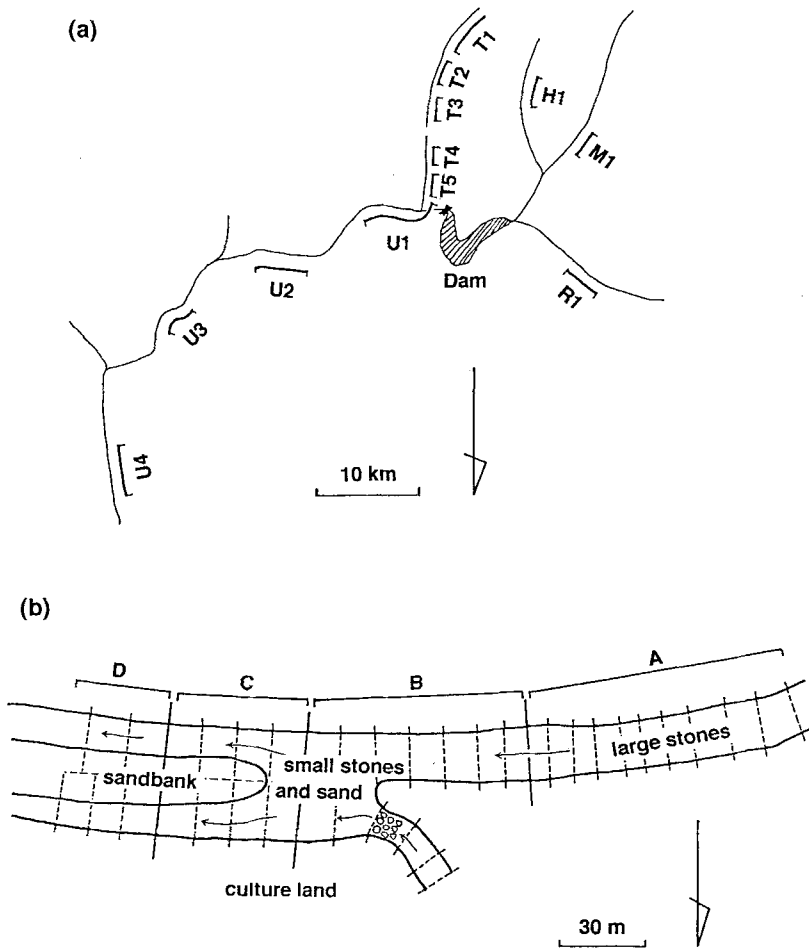
(a)

(b)

Fig. 1. (a) Map of the upper reaches of the Muromi River in 1980. The solid bars indicate the areas where the distribution of damselflies was investigated. In U1, a population census was performed. (b) Schematic map of the study area U1 in 1980. The stream was divided into 33 sections (each 10 m in length). A, B, C and D indicate the habitat segments that the sections were grouped into.

all with different habitat structures (Fig. 1b). The first segment (A) was the uppermost part of the study area. It consisted of a typical mountain stream: trees growing on the banks hanging over the 6 m wide stream with the space near the water surface remaining open. There were sparsely scattered stones and rocks in the stream, and oviposition sites such as mossy stones or dead trees were distributed patchily. The second segment (B) was the middle region, where there was a confluence of two streams. In this segment, there were few oviposition sites. The third segment (C) and fourth segment (D) were located in the lower region of the study area, and contained a small sandbank in the middle of the stream. The width of the stream was about 20 m, including the sandbank. Although segments C and D were open areas, the water surface was covered with stems and leaves from the reed *Phragmites communis*, which was growing on the banks, sandbank and even in the stream. The height of the reeds was about 10 cm at the onset of growth in late April, and reached about 100 cm in the middle of May. The latter period corresponded with the time of the most frequent reproductive activity of *M. pruinosa*.

The population censuses (mark and release method) were performed from 25 April to 22 June in 1980 (15 times), and from 27 April to 10 June in 1981 (16 times). The study area was divided into 33 sections (each 10 m in length), which were grouped into habitat segments A, B, C and D, respectively (Fig. 1b). Adults were captured with an insect net and each was marked on the wings with fast-drying ink. The marked insects were released after recording the degree of maturation, perching height and the section in which they were captured. In subsequent observations of the insects, the above information was recorded for each insect as well as individual numbers but without actually capturing the insects. The behavior of damselflies, such as copulation or oviposition, which were seen during these censuses, were also recorded to determine the frequency of the behaviors in each habitat segment.

In the Muromi river, there is another species, *Mnais nawai*, that also has two male forms: the *nawai* (orange-winged males) and the *sahoi* (pale orange-winged males), and one female form, the *nawai* (pale orange-winged females). Although the male morph of *M. n. f. nawai* was similar to *M. p. f. esakii*, they could be differentiated mainly

by the size of the costal opaque in the forewings (Suzuki 1984).

RESULTS

The distribution of damselflies in the Muromi River

Male density (no. males per 10 m) among the sampling areas in 1980 is shown in Fig. 2a. Data from 1981 were excluded because they were short of sampling areas. The distribution of *M. pruinosa* was biased toward the upper reaches of the river. However *M. nawai* appeared to inhabit the lower reaches of the river. This difference in the distribution of the two species has also been observed by Eguchi (1980). In U1, where the population studies were performed, both species were observed.

The ratio of the two male forms of *M. pruinosa* was examined throughout the Muromi River using data from 1980 and 1981. As shown in
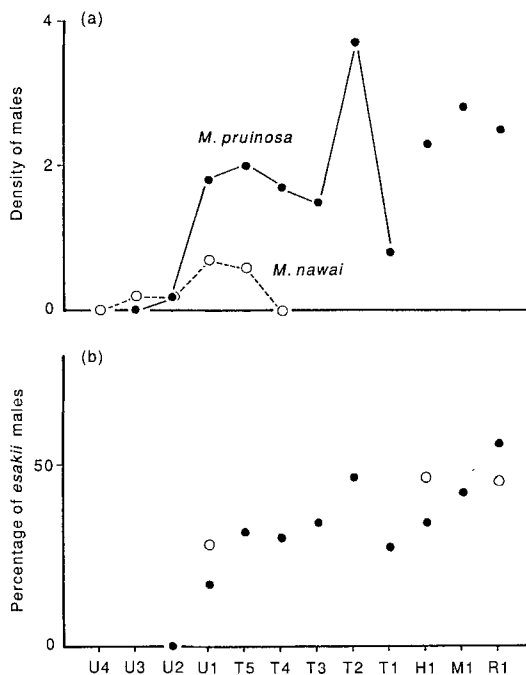

Fig. 2. (a) The average number of males discovered per 10 m at each area in the Muromi River surveyed in 1980. (b) The percentage of *esakii* in the *Mnais pruinosa* male popuulation at 12 areas in 1980 (●) and three areas in 1981 (○).

Fig. 2b, the percentage of *esakii* males to the total male population was apt to increase in the upper stream.

Conditions affecting reproductive success of the two male forms

Seasonal changes in the population density

Seasonal changes in the estimated number of males in U1 in the spring of 1980 and 1981 are shown in Fig. 3a and Fig. 3b, using the Manly and Parr method (Manly & Parr 1968; Manly 1971). The trend of seasonal changes in the number of males was the same for both in 1980 and 1981. *Strigata* males began to emerge in late April, and their density reached a peak in the middle of May and decreased gradually thereafter until the breeding season ended in late June. Although the population density of *esakii* males had a similar seasonal pattern to *strigata* males, the estimation of the first period and the last period of the breeding season could not be done because the rate of recovery was too low. The breeding schedules of *esakii* and *strigata* were observed to be very similar as the number of individuals changed synchronously in both males. The density of the *strigata* males was about two times higher than that of the *esakii* males throughout the breeding season.

Figure 3c shows seasonal changes in the number of females of *M. pruinosa*. The females began to emerge in late April. The emergence time of the females coincided with that of the males. Their breeding season ended in late June.

Territorial behavior and habitat utilization

As in the previous study (Nomakuchi *et al.* 1984), *esakii* males were observed to hold the territory around the oviposition sites, such as moss on the stones in habitat segment A and some open sites in the reed field of C and D. *Strigata* males were always non-territorial and perched on the leaves of trees or reeds in both habitat segments A, and C and D. When the territory of *esakii* males was invaded by *strigata* males, the *esakii* forced *strigata* males out. *Strigata* males escaped without returning the aggression. When neighboring territorial *nawai* males intruded on the territory of *esakii* males while patrolling or pursuing other *strigata* males, *esakii* males fought with them aggressively. The residents usually won.
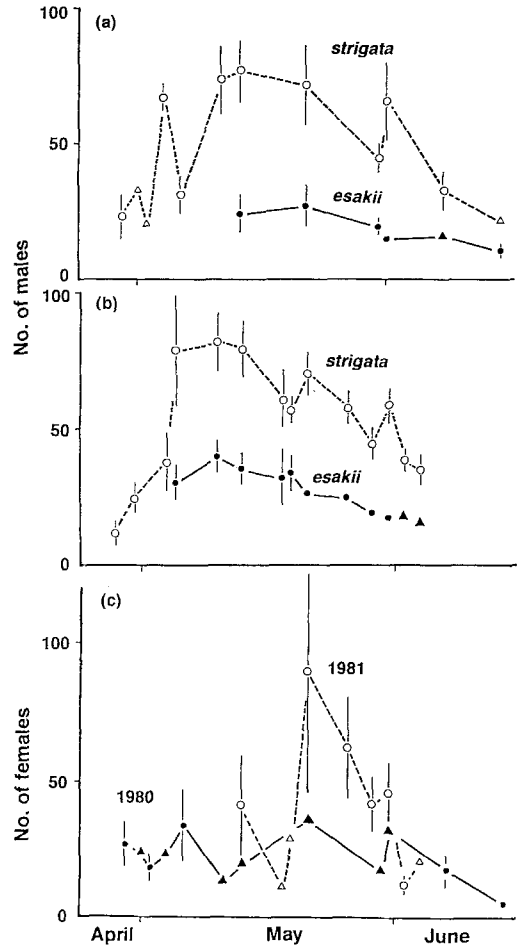

Fig. 3. Seasonal changes in the number of (a) males in 1980, (b) males in 1981 and (c) females in U1. In figure (a) and (b), (———) indicates the number of *esakii* males, and (– – –) indicates the number of *strigata* males. In figure (c), (———) indicates the number of females in 1980 and (– – –) indicates the number of females in 1981. (O, ●) Show the estimates by Manly and Parr's method, and (▲) shows estimates used from the recapture rate calculated at the last day's census, as recapture rate on the relevant day could not be estimated.

At times, it was observed that *strigata* males perched on open sites in the reed field as if they were territorial males. These *strigata* males showed aggressive behavior only toward other approaching *strigata* males. This signified that *strigata* males potentially had the ability to hold a territory if *esakii* males were absent (Nomakuchi *et al.* 1984). However this case was very rare in the study area. Table 1 shows the height of the perching sites of males in C and D habitat segments. Perching sites of *esakii* males were signifi-

Table 1   Height of perching site of males in the lower region of U1 in 1980

Male	Mean height (m)	SD	n
Esakii	0.27	0.46	47
Strigata	0.74	0.73	80

cantly lower than those of *strigata* males (Student's *t*-test, $P < 0.01$). This signifies that *esakii* males always perched nearer to the water surface than *strigata* males because *esakii* males hold their territory.

Environmental structure and habitat utilization

The number of males discovered in the stream varied between each 10 m length section. The cumulative numbers of males and females in all censuses were calculated as an indicator of the degree of the habitat utilization in each habitat segment. Although many males utilized habitat segments A, C and D, few males used B (0.31 individuals per 10 m day^{-1}) because there were no aquatic plants or mossy stones for oviposition sites. Consequently, females also appeared less frequently. Therefore, the patterns of habitat utilization of the two male forms (*esakii* and *strigata*) and females were analysed among three habitat segments, A, C and D. As shown in Fig. 4,
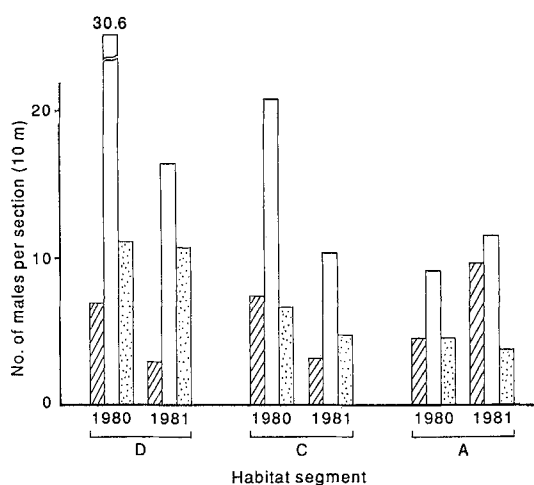

Fig. 4.   The cumulative number of males and females throughout the field censuses in 1980 and 1981. The mean number of adults per section is represented in each habitat segment. (▨) *Esakii* males, (□) *strigata* males, (▣) females.

strigata males frequently used both D and C, but used A less frequently. The frequency of female appearance was also high in habitat segments C and D, but was low in A. This appearance pattern of females was probably due to the abundance of oviposition sites in C and D and the lack of them in A. The similarity of habitat utilization patterns in *strigata* males to those in females is considered to result from the response of *strigata* males to female availability. The habitat utilization patterns of *esakii* males were not similar to *strigata* males and females. *Strigata* males used C and D more frequently than *esakii* males (χ^2 test, $P < 0.01$ in 1980 and $P < 0.005$ in 1981). This signifies that *strigata* males could respond directly to female frequency and remain in D because they were non-territorial, but *esakii* males could not remain there because they were territorial and needed to maintain an open area as their territorial holding. Therefore, *esakii* males were forced to stay in habitat segment A despite limited female availability. This difference in the habitat utilization patterns between the two male forms apparently depends on the different mating strategies (territorial or non-territorial) that each has adopted. This shows that *strigata* males have a higher possibility of encountering females in habitats C and D than *esakii* males.

Competition with other species for territorial sites

Mnais nawai was observed only in the lower region of the study area U1. *Mnais nawai* also has two male forms and one female form, as described previously. *M. n.* f. *nawai* males usually held territories similar to *M. p.* f. *esakii* males, while *M. n.* f. *sahoi* males were non-territorial like *M. p.* f. *strigata* males. However, *M. n.* f. *sahoi* males seldom appeared in the study area. In habitat segments C and D, males of both *M. p.* f. *esakii* and *M. n.* f. *nawai* established their territory separately, with space in between, and non-territorial *M. p.* f. *strigata* males perched on the leaves of reeds around the territories of both species. *Strigata* males often intruded into both species' territories and were repeatedly pursued by territorial owners of both species.

Mnais pruinosa f. *esakii* males and *M. n.* f. *nawai* males competed to establish territories in open areas of the reed field. When *M. p.* f. *esakii* males occasionally entered the territories of *M. n.* f. *nawai* males or *vice versa*, severe aggressions often occurred and the residents usually won. Figure 5a,
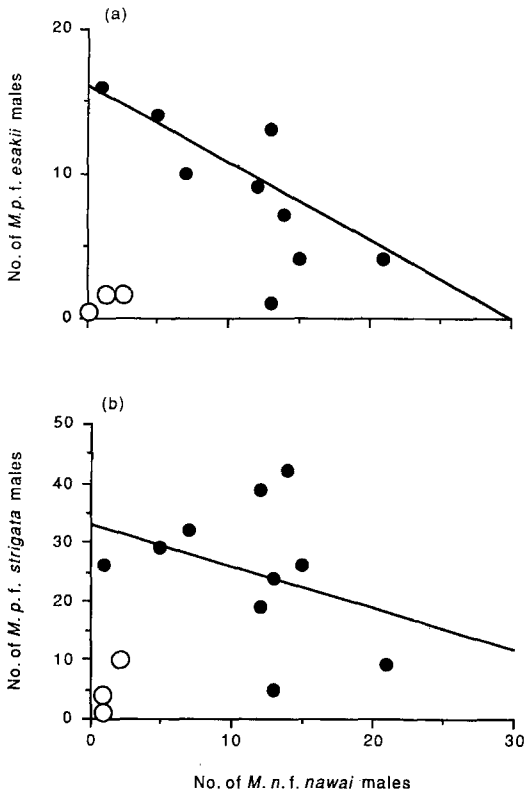
Fig. 5. The correlation of the cumulative number of males of *M. n.* f. *nawai* and (a) *esakii* males, $y = 16.090 - 0.65397x$, $r^2 = 0.588$; and (b) *strigata* males, $y = 33.051 - 0.70360x$, $r^2 = 0.114$. Value of r^2 indicates the coefficient of determination. (O) Indicates the data from habitat sections that both male forms used only occasionally. These data were excluded from the calculation of the regression.

determined by censuses, shows the correlation between the cumulative number of males of *M. p.* f. *esakii* and *M. n.* f. *nawai* in both habitat segments C and D. It uses data from 1980 only because the density of *M. n.* f. *nawai* was very low in 1981. Each point in Fig. 5a indicates the cumulative number of males in each section of habitat segments C and D. Negative correlation between *M. p.* f. *esakii* and *M. n.* f. *nawai* is clear in this figure, probably because of competition for territory. However the correlation between *M. n.* f. *nawai* males and *M. p.* f. *strigata* males is not clear (Fig. 5b). *M. p.* f. *strigata* males utilized any section of habitat segments C and D, whether territorial *M. n.* f. *nawai* males existed or not, probably because *M. p.* f. *strigata* males did not have territory sites and stayed near the territories of *M. n.* f. *nawai*.

Mating success

The difference in the habitat utilization pattern between the two male forms of *M. pruinosa* was checked in relation to their mating frequency. Table 2 shows the total number of copulations from all field censuses in the lower region (habitat segments C and D) and the upper region (habitat segment A) of the study area, respectively. Females copulated with *strigata* males more frequently in the lower region. This may be due to the abundance of *strigata* males in this region. The distribution of copulation frequency of both forms was not significantly different from the distribution of male density of both forms in each region (χ^2 test, $P > 0.1$). The distribution of copulation frequency in both regions was not significantly different from the distribution of male density in both regions in each male form (χ^2 test, $P > 0.1$).

Reproductive success of males must be related not only to copulation frequency but also to efficiency of fertilization of sperm (Siva-Jothy & Tsubaki 1989a,b). Even if a male copulates with a female, its sperm will be removed from the female's reproductive organ when the female copulates with another male before oviposition. Therefore, high copulation frequency does not directly lead to reproductive success of males. The efficiency of fertilization was inferred from patterns of female ovipositions, which have been classified into the following: (ge), (ne), (ns) and (so). (Ge) ovipositions were guarded by territorial *esakii* males, (ne) ovipositions were near territorial *esakii* males, (ns) ovipositions were near *strigata* males, and (so) was a solitary oviposition. Females in the (ge) and (ne) ovipositions were probably fertilized by sperm of the *esakii* males, as the females frequently had begun to oviposit immediately after finishing copulation with *esakii* males, although non-mated ovipositions or ovipositions

Table 2 Frequency of copulations in the upper and lower regions of U1 in 1980 and 1981

Region	Esakii		Strigata		Total	
	1980	1981	1980	1981	1980	1981
Upper	2	5	6	3	8	8
Lower	2	4	14	12	16	16

The distribution of copulation frequency between the male forms in each region or between the two regions in each male form was not significantly different from the distribution of male density (using data from Fig. 4).

after copulating again with *strigata* males occasionally occurred. However (ns) and (so) were probably fertilized by *strigata* males, as females that had copulated with *strigata* males near the stream, in the course of entering the water from the forest or landing on the water, seem to have oviposited without recopulating with *esakii* males. If females, after copulating with *strigata* males, copulate again with *esakii* males, they will be observed ovipositing while guarded by *esakii* males. In habitat segments C and D, oviposition types (ns) and (so) were observed frequently (Table 3). This result suggests that *strigata* males copulated frequently in C and D, and did not suffer sperm displacement from territorial *esakii* males in these habitat segments. In habitat segments A and B, only nine ovipositions were observed in the censuses of 1980 and 1981. Female ovipositions occurred more frequently in C and D than in A and B.

It was expected that the difference in environmental conditions would influence the ratio of the two male forms. The correlation between the environmental conditions and the ratio of *esakii* males to total males was examined at several points in the investigation of distribution. The environmental conditions were classified into three categories by the degree of covering near the water surface: close, intermediate and open (Table 4). Spearman's rank correlation coefficient was highly significant ($P < 0.05$) in determining the degree of covering and the ratio of *esakii* males. This demonstrates that territorial males tended to stay near the open water and non-territorial males stayed near the covered water. However the presence of *M. nawai* males might also have influenced the ratio of *esakii* males, particularly in points U1, U2 and T5, as these two species competed for

Table 3 The number of ovipositions observed in the lower region of the U1

Year	Oviposition category				No. ovipositions
	(ge)	(ne)	(ns)	(so)	
1980	2	2	4	9	17
1981	8	0	2	6	16
Total	10	2	6	15	33
%	36.4		63.6		100

Oviposition guarded by territorial *esakii* (ge), oviposition near the territorial *esakii* (ne), oviposition near the non-territorial *strigata* (ns), solitary oviposition (so).

territorial sites. Assuming that there were no other species in these areas (the author substituted the number of *M. p. f. esakii* for *M. n. f. nawai*, and that of *M. p. f. strigata* for *M. n. f. sahoi*), the correlation was not significant ($P = 0.061$). Therefore, variance of the ratio of *esakii* males to total males could not be explained only by the environmental factor (the covering of the water surface).

DISCUSSION

Mating strategy

Unsolved problems remain in the taxonomical classification of the Japanese genus *Mnais* (Asahina 1976; Suzuki 1984). The present study followed the classification of Suzuki (1984) that suggests this genus has three species with several geographic groups, totalling 13 different forms. *Mnais pruinosa* was one of these three species and has two male forms (*esakii* and *strigata*). In the Muromi river, this species coexists with another species *Mnais nawai*, also belonging to the genus *Mnais* (Fig. 2a).

It has been frequently recognized in Japan that some populations of *M. pruinosa* have two male forms (Suzuki 1984). However a population with only one male form (hyaline wing) has also been found in central Japan, and Siva-Jothy and Tsubaki (1989a,b) reported that this male form had three mating tactics (territory owner, sneaker and opportunist). In this study, there were two male forms in one population. One male form, *esakii* males, always kept to their own territories and captured females entering those territories. Although non-territorial *esakii* males (floaters; Watanabe & Taguchi 1990) were seen in the stream during an initial reproductive period (Nomakuchi & Higashi 1985), in adulthood they were mobile and disappeared in middle and late reproductive periods (Nomakuchi & Higashi 1985). Another form, *strigata*, displayed several mating behaviors as follows: sneaking into *esakii* males' territories to copulate with ovipositing females, intercepting females on branches hanging over the stream (satellites), and waiting for females resting and feeding in the forest area at a distance from the stream. Furthermore, *strigata* males established their own territory when the *esakii* male owner was artificially removed during the

Table 4   The relationship between the ratio of *esakii* to the total male density and environmental conditions in 1980

Habitat segment	U2	U1			T5	T4	T3	T2	T1	H1	M1	R1
		D	C	A								
Conditions	CL	CL	CL	OP	IM	OP	OP	OP	CL	OP	OP	IM
Ratio of *esakii* males to total males	0.0	29.2	16.6	35.4	31.3	41.5	33.3	44.5	26.3	39.5	26.3	49.5
Amended ratio	28.5	39.9	32.7	35.4	31.4	41.5	33.3	44.5	26.3	39.5	26.3	49.5

Environmental conditions are represented by close (CL), intermediate (IM) and open (OP). The amended ratio was calculated substituting the number of *M. p.* f. *esakii* for *M. n.* f. *nawai*, and that of *M. p.* f. *strigata* for *M. n.* f. *sahoi* in order to exclude the effect of *M. nawai*. See the text for details.

field experiment (Nomakuchi *et al*. 1984). Therefore, it is suggested that the strategy of *strigata* males consists of the several mating tactics reported by Siva-Jothy and Tsubaki (1989b). However *esakii* males also have one strategy involving two of these tactics: keeping the territory or temporarily being floaters in the case of a lost battle with other *esakii* for territorial sites.

Although it is not yet clear whether the differences between *esakii* and *strigata* males are genetic, the possibility of genetic differences would seem to be high. The different phenotypes of both forms never have an intermediate type, and never change during the maturation process. Furthermore, as females have only hyaline wings in this population, the phenotype expression may relate to sex chromosomes.

The existence of sperm competitions has been recognized in the mating system of the dragonfly (Waage 1979). This indicates that both the copulation frequency and the rate of fertilization contribute to the reproductive success of males. Therefore, the guarding of females by *esakii* males is designed to prevent them from recopulating with other males and hence to secure fertilization by *esakii* male sperm.

Once the territorial *esakii* male copulates with the female, their guarding behavior usually guarantees fertilization of the eggs. However the copulation frequency appears to depend on them being able to remain at the places where females visit frequently. *Esakii* males avoided places with dense cover and established territories in areas where the water surface was open and oviposition sites were distributed patchily, even if few females visited there (Fig. 4). This indicates that *esakii* males have two fixed behaviors, territorial behavior and the guarding of females after copulation, which are different from *strigata* males. I have called this

behavior by *esakii* males 'guarding strategy' (Nomakuchi *et al*. 1984). *Strigata* males behave as territorial males in the absence of *esakii* males, but they usually adopt several tactics such as sneaking, intercepting females, or waiting in the forest while *esakii* males keep their territory. It appeared that *strigata* males were able to change their mating behavior and stay in the places where females frequently visit, despite being non-territorial males, because of *esakii* males' territorial behavior. This would indicate that *strigata* males attach importance to copulation frequency rather than to securing fertilization by their sperm after copulation. I have called this behavior pattern 'multi-copulation strategy' (Nomakuchi *et al*. 1984). However reproductive success of *strigata* males decreases when the females remate with territorial *esakii* males. Therefore, the environmental conditions around oviposition sites influence the reproductive success of *strigata* males.

Environmental influences on mating strategy

The study area had different environmental structures in the upper and lower regions. The upper region consisted of a typical mountain stream; the water surface was open and oviposition sites such as mossy stones or aquatic plants were distributed patchily. In the lower region, the water surface was covered with reeds and oviposition sites were distributed uniformly. These differences in environmental conditions are considered to influence the habitat choice of both male forms, with their different mating strategies. The upper region provided a good habitat for the *esakii* form because it facilitated territorial holding, while in the lower region it was difficult for the *esakii* males to find females, and to pursue intruding males. *Strigata* males, however, were not influenced by the cover near the water surface in the lower region of the

study area because of their non-territorial behavior.

Females frequently appeared in the lower region of the study area, probably due to the abundance of oviposition sites. Therefore, both male forms were more successful if they stayed in the lower region of the study area, as they had more opportunity to copulate (Parker 1974; Nomakuchi & Higashi 1985). However *esakii* males seemed inclined to keep their territory, despite the time and energy required to search for females and repel intruders, if they remained in the lower region. Most of the *esakii* males, therefore, gathered in the upper region, although a few were able to establish territory in open areas in the lower region. The fact that *M. nawai* appeared only in the lower region of the stream seems to have influenced the decrease in the density of *esakii* males in this region. Most of the *strigata* males stayed in the lower region, but the density of the *strigata* males also seems to be limited by the male–male competition for females.

The differences of habitat utilization between the two male forms may influence the mating frequency of both. Although copulations of *strigata* males occurred more frequently than *esakii* males in the lower region, the distribution of the copulation frequency between the two male forms was not different from that of their density. This suggested that copulations occurred in proportion to the ratio of male forms in both upper and lower regions.

In the lower region (habitat segments C and D) of the study area, oviposition sites (stems of *Phragmites communis*) were distributed rather uniformly and *esakii* males occupied only a few of the oviposition sites there. Therefore, the probability of females visiting oviposition sites in the territory of *esakii* males in the lower region seems to be smaller than that in the upper region (habitat segment A). Actually, female single ovipositions without guards occurred frequently in the lower region. The females that copulate with *strigata* males appeared to lay eggs fertilized by *strigata* males' sperm. As females copulate with *strigata* males more frequently, eggs fertilized by *strigata* males seem to be laid more abundantly than those fertilized by *esakii* males in the lower region during adult season.

It appears that the selection of *esakii* and *strigata* males is frequency-dependent, because competition for reproductive success occurs within the same forms (Christiansen 1988; Maynard Smith 1989). This selective force may generate the variable equilibrious ratio between the two male forms according to differences in environmental conditions and competition with other species. In U1, a selection of the two male forms, favoring the equilibrious ratio biased toward *strigata*, seemed to operate in the lower region (habitat segments C and D). From the distribution of males throughout the Muromi River, the ratio of *esakii* males to total males increased in the upper areas. This result probably reflects the equilibrious ratio of the two male forms swinging toward *esakii* males under the frequency-dependent selection according to the different environmental conditions in which *esakii* males easily hold their territory. However the ratio of the two forms in each area of the Muromi River may be determined not only by the frequency-dependent selection of the two male forms but also by the movement of males. On the other hand, Nomakuchi *et al.* (1988) reported a population on a stream in the Ino River, which is about 20 km away from the Muromi River, where the density of *esakii* males was twice that of *strigata* males. The Ino River's water surface was open and oviposition sites were distributed patchily. The form ratio between the two rivers differed because of the frequency-dependent selection of the two male forms. The different equilibrious form ratio was favored because of the small movement of males between the two rivers.

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