

AN EXPERIMENTAL STUDY OF THE TERRITORIALITY IN *MNAIS PRUINOSA PRUINOSA* SELYS (ZYGOPTERA: CALOPTERYGIDAE)*

S. NOMAKUCHI¹, K. HIGASHI², M. HARADA³ and M. MAEDA¹

¹ Department of Biology, Faculty of Science, Kyushu University,
Fukuoka 812, Japan

² Department of Biology, Faculty of Liberal Arts, Saga University,
Saga 840, Japan

³ Department of Pathology, Kagawa Medical School, Takamatsu 760,
Japan

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Two forms of *M. p. pruinosa* males occur in the study area (Ino river, Japan), viz. f. *esakii* and f. *strigata*. Territorial behaviour between *strigata* and *esakii* males is initiated only by the latter; and usually leads to displacement of *strigata*. The behaviour of *strigata* males in the absence of *esakii*, was observed following removal of *esakii* males from the experimental area. *M. p. p. strigata* males established territories, and drove away other intruding *strigata*. They also showed the same reproductive behaviour (except courtship) as *esakii* males when females appeared in the territory. The mean frequencies of copulations observed for *strigata* males under natural and experimental conditions were 1.0 ± 1.2 (95% confidence limits) times and 1.1 ± 1.1 times per 20 min, respectively. This suggests, therefore, that the frequency of copulations for *strigata* does not increase when *esakii* males are removed. The pre- and post-copulatory mating strategies of both *esakii* and *strigata* males are discussed.

INTRODUCTION

During recent years it has become clear that there are often several strategies used within the same species to compete for a mate, a nest site or some other scarce resource (KREBS & DAVIES, 1981). Territorial males of field cricket, *Gryllus integer*, call by rubbing their forewings (callers), while other males

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(satellites) sit silently near the callers and attempt to intercept females as they arrive (CADE, 1979). Territorial males of dragonfly, *Sympetrum parvulum*, perched on the grasses, seize females appearing in the territories and accomplish the copulation position in the air, while wandering males often grasp females elsewhere, outside of the oviposition sites, and they come to the water in copula (UÉDA, 1979).

Mate competition occurs both before and after copulation or sperm transfer. Precopulatory mating competition is often characterized by aggression, as in territoriality or dominance behaviour, by which males actively prevent other males from mating (CADE, 1979). Postcopulatory sperm competition is reported by PARKER (1970) for some insects and by WAAGE (1979a, 1982) and MILLER & MILLER (1981) for dragonflies.

In the study area, two forms of *Mnais p. pruinosa* males occur, orange- and hyaline-winged males (f. *esakii* and f. *strigata*; ASAHINA, 1976), and only one female form with hyaline wings. Territorial behaviour between *strigata* and *esakii* males is initiated only by the latter, and usually leads to displacement of *strigata* (HIGASHI, 1976, 1981). In this paper we show how *strigata* males behave when the *esakii* are absent from the stream, and discuss the mating strategies of both types of males.

STUDY AREA AND METHODS

This study was carried out in the upper reaches of the Ino River (cf. HIGASHI, 1976, 1981; HIGASHI et al., 1979).

Observations were made on the territorial and reproductive behaviours of selected marked individuals for 20-minute periods at one-hour intervals during the 1979 flying season. Frequencies of activities such as circle flight, rocking flight, courtship, and guarding were carefully observed and recorded separately, and differences in the behaviours between the males of *esakii* and *strigata* were analyzed.

In order to know whether or not *strigata* males establish territories when the territorial males of *esakii* are absent, all of the *esakii* males were captured every day from a 500 m length of the stream. Then, the behaviours of *strigata* males were observed.

OBSERVATIONS

TERRITORIAL BEHAVIOUR IN MIXED POPULATIONS

The territories of *esakii* males and the location of *strigata* males at 14:46, 30 May in 1979 are shown in Figure 1. The *esakii* males (No. 161, No. 269 & No. 294) established perching sites and territories. However, *strigata* males (No. 296 & No. 298) only perched on tree branches hanging over the stream, and sometimes flew down to the stream and patrolled the territories of *esakii* males, at 5-10 cm height above water surface. The territorial *esakii* males flew quickly toward the

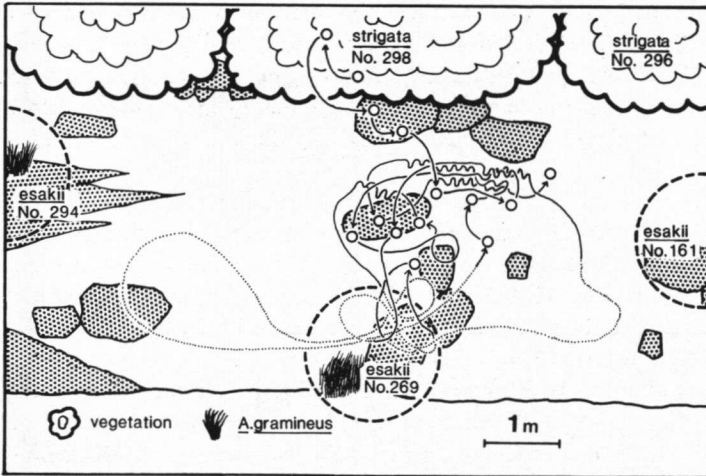


Fig. 1. The flight path of a nonterritorial *strigata* (No. 298) during 20 minutes. Territories of *esakii* are shown schematically. The small circles indicate perching sites of No. 298. Solid and dotted lines indicate the flight path of No. 298 and that of No. 298 pursued by *esakii* (No. 269), respectively. Wavy lines indicate the searching behaviour for a mate. The *esakii* males (No. 269, No. 294 and No. 161) are territorial.

intruding males and pursued them. Figure 1 shows the flight path for one such encounter (male No. 298). The intruding male escaped and after a few minutes perched on plants growing along the stream. The nonterritorial *strigata* males remained in the same area and repeated these intrusions for several days. The same pattern of intrusions was observed for nonterritorial *esakii* males, although most of them usually dispersed to other areas.

EXPERIMENT EXCLUDING *ESAKII* MALES

In order to know how *strigata* males behave when *esakii* males are absent, all of the latter (131) were removed (9 to 24 May) and the behaviour of *strigata* males (8) was observed in the experimental area.

The flight path of a male *strigata* (No. 166) is shown in Figure 2a. He perched on the same stones after patrolling or pursuing. When a female appeared there, he copulated with her without courtship and guarded her during oviposition. The same behaviour was observed in four other males of *strigata* in the experimental area. The behaviour of these was similar to that of territorial *esakii* males. (Out of eight *strigata* males, four were territorial, and two were nonterritorial; the latter were pursued by the territorial individuals). We conclude, therefore, that *strigata* males become territorial in the absence of *esakii*.

The territorial behaviours of *esakii* and *strigata* males are described later and compared for both males.

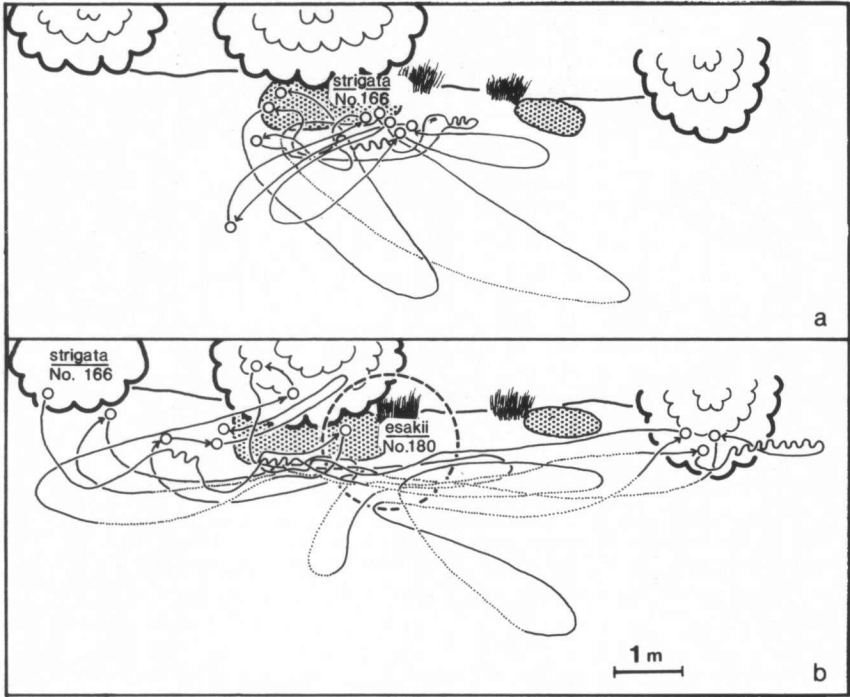


Fig. 2. The flight path of the male *strigata* (No. 166): (a) The territory of No. 166 in the experimental area, when all of the *esakii* males were excluded. Dotted lines indicate the flight path of No. 166 pursuing the other male *strigata*. — (b) The flight path of No. 166 after releasing the *esakii* male (No. 180). Dotted lines indicate the flight path of No. 166 pursued by No. 180.

A territorial *esakii* male (No. 180) was captured upstream from the experimental area, and released near the territory of a *strigata* male (No. 166). Figure 2b shows the flight path of No. 166 after releasing No. 180. When the *esakii* male (No. 180) appeared near him, he flew quickly toward No. 180. They hovered at a moment facing each other, and No. 180 pursued him. The *strigata* male was pursued for some time around his territory and escaped into the tree branches. The *esakii* male then perched on the stone where No. 166 had perched before, and established a territory. Male No. 166 repeatedly intruded into the territory of No. 180 and was pursued each time. These facts suggest that a *strigata* male is able to establish a territory if *esakii* is absent, but is prevented from doing so when *esakii* males are present.

AGGRESSIVE INTERACTIONS AMONG THE MALES

Aggressive interactions observed among the males *M. p. pruinosa* have been classified into several patterns (HIGASHI, 1981). These interactions were reclassified into five intensity levels with reference to the works of JACOBS (1955), PAJUNEN (1964, 1966a, 1966b), UBUKATA (1979), ARAI, (1982) and HIGASHI & UÉDA (1982) as follows: (A) one male pursues the other unilaterally; (B) two males pursue each other, then suddenly change their flight route; (C) their flight route sometimes forms concentric loops, consisting of a succession of sharp turns within a limited area (circle flight); (D) following a circle flight, they sometimes fly up gradually to ca 1.5 m height, hovering parallel with each other and making sudden climbs and return dives of ca 30 cm (rocking flight); and (E) occasionally during the rocking flight, two males fly quickly upward to the height of ca 10 m (dual flight). These five components (A-E) are arranged in increasing order of behavioural intensity.

Table I
Frequencies of the pattern of aggressive behaviours observed among the interacting males of *Mnais pruinosa pruinosa*

Interacting males	Pattern of aggressive behaviours				
	A	B	C	D	E
ES - ES					
(1) ter - ter	3 (5)	9 (8)	0 (1)	0 (0)	1 (0)
(2) ter - non	35 (15)	22 (8)	2 (6)	5 (3)	5 (3)
ES - ST					
(3) ter - non	125 (57)	4 (2)	0 (0)	0 (0)	0 (0)
ST - ST					
(4)* ter - non	10	43	34	2	2
(5) non - non	1	11	9	1	3

ES: f. *esakii*; — ST: f. *strigata*; — ter: territorial male; — non: nonterritorial male; — (): observations in 1978; — * Experimental condition. (For explanation of pattern of aggressive behaviours cf. text).

The observed frequency of each pattern is shown in Table I. The unilateral pursuit of *strigata* males by *esakii* was observed in overwhelming frequency. Therefore *esakii* males are dominant over *strigata* in territory holding, as reported by HIGASHI (1976). In two cases, (1) and (3) of this Table, the highest intensity levels, (D and E), were not observed. This fact suggests that (1) territorial *esakii* males do not fight aggressively with neighboring territorial *esakii*, and (2) nonterritorial males of *strigata* give up quickly in fights with territorial *esakii*, perhaps because they take other alternative strategies for mating, as will be described later.

To compare the aggressive behaviours of the two forms (2 and 4, in Table I) and those between normal and experimental *strigata* (4 and 5), the patterns of behaviour were first grouped as weak (A and B) and intense (C-E). The difference between the forms (Tab. I; 2 and 4) is significant ($p < 0.05$). This result suggests that nonterritorial males of *strigata* fight more aggressively with territorial *strigata* than do *esakii* territorial and nonterritorial males. The difference between the two *strigata* groups of males (Tab. I; 4 and 5) is not significant ($p > 0.05$). This result shows that nonterritorial *strigata* male fights to occupy the suitable perch sites are equally intense with both territorial and nonterritorial *strigata*.

REPRODUCTIVE BEHAVIOURS OF TERRITORIAL AND NONTERRITORIAL MALES

The reproductive behaviour of *M. p. pruinosa* has been reported briefly by HIGASHI (1976) and in more detail by HIGASHI (1981). We compare the differences among the behaviours of territorial *esakii* and *strigata* and nonterritorial *strigata*. When a female appears in the territory of an *esakii* male and perches on an emerged plant (*Acorus gramineus*), he flies quickly to her, courts in front of her, and then enters the tandem position. Copulation follows immediately or after flying around in tandem. The copulation duration was 69.3 ± 30.2 ($n=15$, 95% confidence limits) seconds. After separation they rest for a moment, and the female then begins to oviposit into *A. gramineus* or moss on stones in the male's territory. During the oviposition he guards her. During this guarding, when another female appears in the territory and begins to oviposit, the male occasionally guards her without copulation.

Nonterritorial *strigata*, although sometimes pursued by *esakii* males, quickly fly toward ovipositing females in the *esakii* male's territory and take them in tandem position without courtship. They fly up in tandem to trees above the stream to escape from pursuing territorial *esakii* and then copulate. The copulation duration was 100.0 ± 62.1 sec ($n=7$). After separation they rest there for a moment and the female flies away without oviposition, and the male tries to follow her.

The reproductive behaviour of territorial *strigata*, when *esakii* males were removed, was unlike that of *esakii*. When a female appeared in the territory, the male approached her quickly and took her in tandem position without courtship. They copulated immediately in the territory or after flying around it in tandem. The copulation time was 78.4 ± 33.6 ($n=11$) sec. After separation they rested for a moment. When the female began to oviposit in the territory, the male guarded her oviposition, that is, when other *strigata* intruded and approached her, he attacked and pursued approaching *strigata*. The female flew away after oviposition. Therefore, the reproductive behaviour of territorial *strigata* is similar to that of territorial *esakii*, except for the courtship behaviour.

The frequency of copulation per 20 min varied little for the three contexts

described above: territorial *esakii* (1.4 ± 1.4 , $n=9$), nonterritorial *strigata* (1.0 ± 1.2 , $n=28$) and territorial *strigata* (1.1 ± 1.1 , $n=21$). This result suggests that the frequency of copulation of *strigata* does not increase if they establish their territories.

DISCUSSION

Several odonate species are known or expected to be capable of sperm displacement — the removal or repositioning of some or all of the sperm of previous males prior to fertilization (WAAGE, 1979a, 1982; MILLER & MILLER, 1981; MILLER, 1982). Therefore, the males of *M. p. pruinosa* are exposed not only to the competition for mates but also to sperm competition. The differences in the territorial and reproductive behaviours between the males *esakii* and *strigata* seem to be related to both contexts competition. In order to gain reproductive success, it is necessary for both *esakii* and *strigata* males to copulate with as many females as possible and also to keep these females mated from re-mating with other males.

When mates or resources are patchily distributed some individuals may be able to defend more mates or better quality resources (e.g. nest sites, food; KREBS & DAVIES, 1981). In the study area *Acorus gramineus* and mossy stones were used as oviposition sites and were patchily distributed in the stream. Such a patchy distribution of oviposition sites appears economically defensible (BROWN, 1964). The *esakii* males established their territory and waited for the appearance of females. As a result of precopulatory mating competition, it seems that some males could occupy a suitable oviposition site (many females appeared there) while others were forced to occupy an unsuitable one (few females appeared there). Although *strigata* males could establish territories in the absence of *esakii*, they were nonterritorial and stayed around the territory of *esakii* in natural conditions (e.g. as satellite males; ALCOCK, 1982). It would seem that the *strigata* males should establish territories around less suitable oviposition sites, because these sites are not always occupied by *esakii*. However they do not and this needs explanation. It appears to be related to the frequency of female appearances. The *strigata* males search for females in and near the territories of *esakii* males, where many females appear. Moreover, to increase the chance of copulations, *strigata* males intrude repeatedly into *esakii* territories, and try to copulate with the females ovipositing there (sneak mating tactic).

The *esakii* males characteristically guard ovipositing mates. This behaviour seems to be a countermeasure to the sperm competition interactions, by doing so they protect their own sperm in the bursa copulatrix and spermatheca of the females from displacement by other males (e.g. WAAGE, 1979b; CORBET, 1980; ALCOCK, 1982). However, *strigata* males did not guard females after copulation. This means that whether or not their sperm can fertilize the eggs is

quite dependent on the oviposition conditions of the female (whether or not she copulates again with other males before she oviposits). In spite of this handicap, they appear to stay around the *esakii* territories and search for the females in order to increase their opportunity of mating. Therefore, their behaviour can be considered as a multicopulation strategy. In the *esakii* males, courtship behaviour is frequently observed. However, *strigata* males attempt tandem with females without courtship. This behaviour of *strigata* may function to prevent the refusing behaviour of females.

In the field, very intense aggressive behaviour is observed between the territorial and nonterritorial *esakii*, and between the nonterritorial *strigata* males (C-E, in Tab. I). This appears to indicate intense competition for oviposition sites among *esakii* males and for the space around *esakii* territories by nonterritorial *strigata* males even though the space does not seem economically defensible. UBUKATA (1979) and ARAI (1982) observed that also territorial and nonterritorial *ogumai* of *M. p. costalis* aggressively fight each other.

In the study area, the oviposition sites are distributed patchily and there is little visual interference such as a thicket of aquatic plants in the space above the water surface. Therefore, the *esakii* males can efficiently detect and drive out intruding males from their territories and can easily find approaching females. The same phenomenon is observed for *M. p. costalis* (UBUKATA, 1979). Environmental conditions in the study area seem, therefore, to give the advantage to the *esakii* males, and this seems to affect the number of both males, *esakii* and *strigata*, in the study area. Population studies in the study area show that the density of *esakii* during the study periods is about two times higher than that of *strigata* (HIGASHI, 1976; and unpublished).

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