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ALTERNATIVE MATING TACTICS AND AGGRESSIVE MALE INTERACTIONS IN *MNAIS NAWAI* YAMAMOTO (ZYGOPTERA: CALOPTERYGIDAE)

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Two forms of *M. nawai* males occur in the study area, viz. the orange wing (f. *nawai*) and the pale orange wing (f. *sahoi*). The *nawai* males defend a territory and copulate with females that appear in their territory, while *sahoi* males are non-territorial and sneak matings with females that are ovipositing in a territory. Observations of aggressive behaviour among the males suggest that the non-territorial *sahoi* relinguish in fights with the territorial *nawai*, perhaps because they adopt other alternative mating tactics (e.g. sneaking). The frequencies of copulations observed for *nawai* and *sahoi* were 35 and 12, respectively. The ratio of these frequencies to population size of each of the 2 morphs was not significant. Therefore, the reproductive success of *sahoi* males is influenced by the female oviposition condition. The pre- and post-copulatory mating tactics of both *nawai* and *sahoi* males are discussed.

INTRODUCTION

Discrete morphologies exist in a wide range of species, and frequently play an important role in the ability to defend a territory or to acquire mates (CRNOKARAK & ROFF, 1995). Intraspecific dimorphisms associated with such behaviour patterns in Odonata include differences in male wing colour, e.g. in *Mnais pruinosa* (NOMAKUCHI et al., 1984) and in *M. pruinosa costalis* (WATANABE & TAGUCHI, 1990). On the other hand, the male body size and/or age may influence success in aggressive interactions and the tactics to secure mates (*Nannophya pygmaea*, TSUBAKI & ONO, 1987 and *Calopteryx maculata*, FORSYTH & MONTGOMERIE, 1987).

Mate competition occurs both before and after copulation or sperm transfer. Precopulatory mating competition is often characterized by aggression as in territoriality or dominance behaviours (CADE, 1979). Post-copulatory sperm compe-

tition was reported by PARKER (1970) for some insects and by WAAGE (1979), MILLER & MILLER (1981) and SIVA-JOTHY (1987) for dragonflies. In Japanese *Mnais*, alternative mating tactics were detected by NOMAKUCHI et al. (1984) for *M. p. pruinosa* (territorial and sneak mating tactics), by NOMAKUCHI (1992) for *M. pruinosa* (guarding strategists and multi-copulation strategists), by UBUKATA (1979) and WATANABE & TAGUCHI (1990) for *M. p. costalis* (territorial and sneaky mate securing tactics). Post-copulatory sperm competition was reported by SIVA-JOTHY & TSUBAKI (1989a, 1989b) for *M. p. pruinosa*.

In the study area, there are two wing colour forms of *Mnais nawai* males, the orange-winged f. *nawai* and the pale orange-winged f. *sahoi* (ASAHINA, 1976), but only a single female form with pale orange wings (f. *nawai*). NOMAKUCHI et al. (1996) stated that the mating tactics of *nawai* and *sahoi* males are territorial and non-territorial, respectively. In this paper we show differences in the aggressive behaviours between the two male forms and discuss the pre- and post-copulatory mating tactics in both male forms.

STUDY AREA AND METHODS

This study was carried out at the confluence of the main and tributary streams of the Muromi River, located about 12 km from the mouth of the river (cf. HIGASHI & UEDA, 1982; NOMAKUCHI, 1992). The river flows through the western part of Fukuoka City, Japan.

Observations were made on the territorial and reproductive behaviours of selected marked individuals for 20-minute periods at one-hour intervals during the 1988 flying season. Frequencies of activities, such as circle flight, rocking flight and dual flight, were carefully observed and recorded separately, and differences in the behaviours between the males of *nawai* and *sahoi* were analyzed. The observation of copulation frequencies and the population censuses (mark and release method) were performed in 1989. Data from 1984 and 1987, related to copulation frequencies and population censuses, were also used.

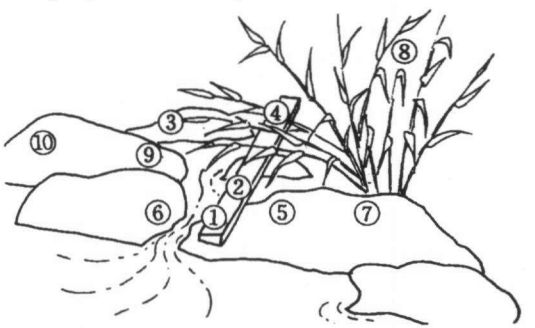

Fig. 1. Perching sites of territorial and non-territorial males at oviposition site (dead wet wood). – ① ②& ④: oviposition material (dead wet wood); – ③ ⑤ ⑥ ⑦ ⑨& ⑩ : rocks; – ⑧ : reeds.

RESULTS

RELATIONSHIP BETWEEN *NAWAI* AND *SAHOI* MALES

The *nawai* males established territories containing perching sites and oviposition substrates (e.g. dead wet wood). However, *sahoi* males only perched on rocks or the reed, *Phragmites japonica*, and sometimes patrolled the *nawai* territories to search for females (NOMAKUCHI et al., 1996). To show the relationship between *nawai* and *sahoi* males, the sequential changes in perching sites of both male forms around the oviposition substrates (dead wet wood) are shown in Figure 1. Individuals of the two male morphs observed at the perching sites were recorded at intervals of five minutes, in principle (Fig. 2). Although another species, *M. pruinosa*, inhabits this area and sometimes appears around this oviposition substrate, individuals of *M. pruinosa* (one *strigata* male and one female) were omitted from this figure, to avoid complexity. This figure shows that four *nawai* males were territorial and successively occupied perching sites 2, 3, 4 and 5, respectively, and three *nawai* males and two *sahoi* males were non-territorial and stayed around the *nawai* territories for at least one hour. This figure also shows that when females began to oviposit at an oviposition site, the non-territorial *nawai* and *sahoi* males frequently intruded into the territories, though they were pursued by the territorial males.

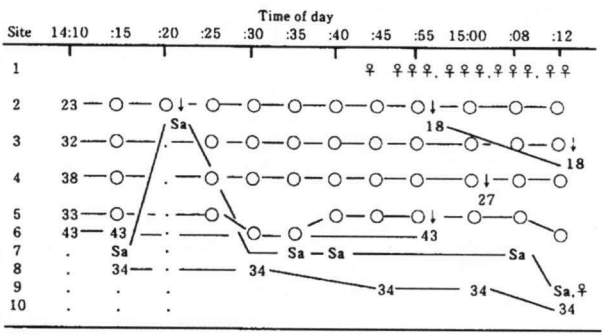

Fig. 2. Sequential observations of perching sites of territorial and non-territorial males at oviposition site. – [Site numbers indicate the perching sites of the territorial and non-territorial males (cf. Fig.1). Individual numbers of *nawai* and *sahoi* (No. 18) males are shown by Arabic numerals. Territorial males are shown by small circles. No mark *sahoi* male and females are shown by Sa and ♀, respectively. Arrows indicate the pursuing behaviour of the territorial males].

In some dragonfly species, larger males have been found to be more successful in attaining a territory; *Orthetrum chrysostigma* (MILLER, 1983) and *Megaloprepus coerulatus* (FINCKE, 1984). In *M. nawai*, the hind wing lengths of *nawai* and *sahoi* males were 40.3 ± 1.2 in mm (n = 50, mean ± s.d.) and 37.8 ± 1.1 (n = 35), respectively. The wing length of *nawai* males was slightly larger than that of *sahoi* males. However, the fact that almost all of the *sahoi* males were non-territorial, may suggest that the territory ownership is not affected by body size but rather by male dimorphism.

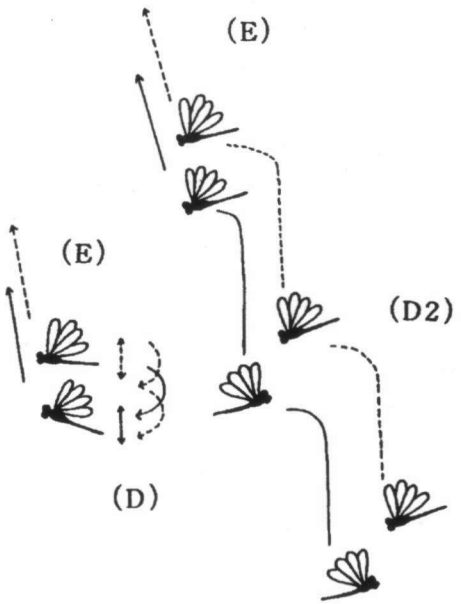

Fig. 3. Schematic illustration of aggressive behaviour in *M. nawai* and *M. pruinosa*. – (D), (D2), (E): patterns of aggressive behaviour, rocking and dual flights (cf. Tab. I). – [See text for detailed explanation].

Table I

Frequencies of aggressive behaviour patterns observed among interacting *Mnais nawai* males

Interacting males	Patterns of aggressive behaviour A	B	C	D2	E
naw - naw					
(1) ter - ter	10	56	2		
(2) ter - non	57	18	6	37	20
naw - sah					
(3) ter - non	176	1			
sah - sah					
(4) non - non	26	4	11	6	2

naw: *nawai* male, sah: *sahoi* male, ter: territorial male, non: non-territorial male

AGGRESSIVE BEHAVIOURS

Aggressive interactions observed among *M. nawai* males were classified into five intensity classes, as described by NOMAKUCHI et al. (1984), after the works of JACOBS (1955), PAJUNEN (1964, 1966a, 1966b), UBUKATA (1979), HIGASHI (1981), HIGASHI & UEDA (1982), ARAI (1982) and SUZUKI (1985). The five patterns were as follows (Fig. 3): (A) one male pursues the other unilaterally; (B) two males pursue each other, then suddenly change their flight route; (C) the flight route sometimes forms concentric loops, consisting of a succession of sharp turns within a limited area (circle flight); (D2) following a circle flight, they sometimes gradually fly up to a height of ca 1.5 m hovering and facing each other (this behaviour is usually repeated 2-3 times), and hovering parallel with each other, 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 a height of ca 10 m (dual flight). These five components (A-E) are arranged in increasing order of behavioural intensity. The rocking flight behaviour (D2) differed slightly from that in *M. p. pruinosa* (NOMAKUCHI et al., 1984). Namely, the rocking flight in *M. p. pruinosa* was performed at approximately the same

height, while that in *M. nawai* was performed by changing the height two or three times. The *M. p. pruinosa* study area (NOMAKUCHI, et al., 1984) is a mountain stream that is almost entirely covered by a crown of trees, and that of *M. nawai* is a river of ca 10 m width with open area above it. Therefore, it is considered that the rocking flight of *M. nawai* can be performed over wide ranges both horizontally and vertically.

The observed frequency of each pattern is shown in Table I. The unilateral pursuit of *sahoi* males by *nawai* was observed with overwhelming frequency. Therefore, *nawai* males are dominant over *sahoi* in territory holding, as reported by NOMAKUCHI et al. (1996). In two cases, (1) and (3) in Table I, the highest intensity levels (D2 and E) were not observed. This suggests that (1) the territorial *nawai* males do not fight aggressively with the neighbouring territorial *nawai*, and (2) the non-territorial *sahoi* males relinquish quickly in fights with the territorial *nawai*, perhaps because they use other, alternative mating tactics.

To compare the aggressive behaviours of the two male forms (2 and 4, in Tab. I), the patterns of behaviour were grouped as weak (A and B) and intense (C-E). The difference between the forms was not significant (χ^2-test, $p>0.05$). This suggests that the non-territorial *nawai* males fight more aggressively with the territorial *nawai*, and that the non-territorial *sahoi* males fight with each other to occupy suitable locations around the territories of *nawai* males.

REPRODUCTIVE BEHAVIOUR

The reproductive behaviour of *M. nawai* has been briefly described by NOMAKUCHI et al. (1996). We compared the differences between the behaviours of the territorial *nawai* and the non-territorial *sahoi*. When a female appeared in the *nawai* territory and perched on an oviposition site or a rock near an oviposition site, the male quickly flew to her, courted briefly in front of her, and then entered the tandem position. Copulation followed immediately or after flying around in tandem, and the mean copulation duration of *nawai* males was 119.6 ± 76.2 s ($n = 41$). After separation, the pair rested for a moment, and the female then began to oviposit into dead wet wood or the reed stems in the male's territory. The male guarded the female throughout oviposition. During this guarding, if another female appeared in the territory and began to oviposit, the male occasionally guarded her without copulation (cf. Fig. 4).

The non-territorial *sahoi*, although sometimes pursued by *nawai* males, quickly flew toward ovipositing females in the *nawai* territory and took them in the tandem position without courtship. Two types of this behaviour were observed. First, the pair flew up in tandem to reeds to escape from pursuing the territorial *nawai* and then copulated. After separation, they rested there for a moment, the female flew away without oviposition, and the male tried to follow her. In the second type, they copulated on the oviposition substrate. In this case, the territorial *nawai* sometimes

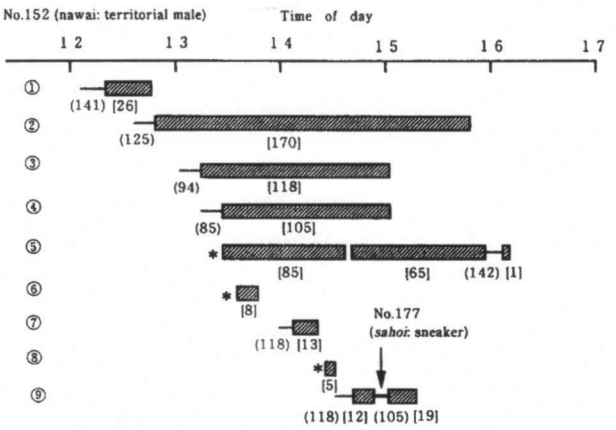

Fig. 4. Records of copulation and oviposition duration in the territory of No. 152 male (*nawai*). – ( ): copulation in seconds; – [ ]: oviposition duration in minutes; – *: guarding without copulation. – ① - ④ show respective females, but it is not known whether ⑤ - ⑨ females are the same as ① - ④ females, since ⑤ - ⑨ were not marked, some of these females may not actually represent separate individuals.

did not pursue the copulating *sahoi*. After copulation, the female continued the oviposition and the territorial *nawai* guarded her (cf. Fig. 4). The mean copulation duration of *sahoi* males was 129.8 ± 54.6 s (n = 13). Although the *sahoi* copulated on the oviposition substrate or the leaves of reeds, the copulation durations in each case were not distinguished in this study.

The record of copulation and guarding behaviours of the territorial *nawai* males and the sneaking behaviour of *sahoi* males in a territory is shown in Figure 4. A brief explanation of this figure is as follows: The first female appeared at 12:15 p.m. and a territorial *nawai* male (No. 152) copulated with her (141 s). She continued oviposition for 26 min and No. 152 male guarded her. The fifth female appeared at 13:30 p.m. and began oviposition, but the male did not copulate with her and she oviposited for a total 134 min. In this case, it may be considered that she oviposited eggs fertilized by another male's sperm. The ninth female appeared at 14:15 p.m. and No. 152 male copulated with her (178 s). The *sahoi* male (No. 177) sneaked to the ovipositing female (oviposited for 12 min) and copulated with her on an oviposition substrate. After copulation, she continued oviposition for 14 min. In this case, it is considered that she oviposited eggs fertilized by the sperm of No. 177 male. These observations suggest that *sahoi* males have the opportunity to fertilize eggs with their sperm, because of the altruistic behaviour of the territorial *nawai* males, though succesful copulations by sneak tactics of *sahoi* males were only observed a few times.

The copulation frequencies of the territorial *nawai* males and the non-territorial *sahoi* males were 35 and 12 times (totals for 1984 and 1989), respectively. While, the total numbers of marked individuals of the two male forms were 131 and 50 (totals for 1984 and 1989), respectively. Therefore, the frequencies of copulations per individual of each male form were 35/131 and 12/50, respectively. The difference between these ratios was not significant (normal approximation method, $p>0.05$). In other words, the sneak tactics of *sahoi* males affords the same copula-

tion opportunities as the territorial tactics of *nawai* males.

DISCUSSION

AGGRESSIVE BEHAVIOURS AND MATING TACTICS

When mates or resources are patchily distributed, some individuals may be able to defend more mates or better quality resources (e.g. oviposition sites, nest sites; KREBS & DAVIES, 1981). In the study area, dead wet wood and stems of the reed, *Phragmites japonica*, were used as oviposition substrates. However, females frequently oviposited into wet dead wood which was scattered in the river and was patchily distributed. Such a patchy distribution of oviposition sites appears economically defendable (BROWN, 1964). The *nawai* males established their territory and waited for the appearance of females (cf. *M. p. pruinosa*: NOMAKUCHI et al., 1984). As a result of precopulatory mating competition, some males could apparently occupy a suitable oviposition site (many females appeared there), while others were forced to occupy an unsuitable one (few females appeared there). On the other hand, the *sahoi* males were non-territorial and stayed around the *nawai* territories, searching for females in and near the territory. The difference in behaviours of the two male forms was the mating tactics, i.e. territorial (*nawai*) and sneaking (*sahoi*) tactics, as will be discussed below.

In the field, very intense aggressive behaviour was observed between the territorial and non-territorial *nawai* males, and between non-territorial *sahoi* males (C-E, in Table I). This appears to indicate an intense competition for oviposition sites among *nawai* males and for perching sites around *nawai* territories by the non-territorial *sahoi* males, even though the perching site does not seem economically defendable. Unilateral pursuit of *sahoi* males by *nawai* was observed with overwhelming frequency. This suggests that *sahoi* males relinquish quickly in fights with territorial *nawai*, perhaps because they adopt alternative mating tactics. In other words, the *sahoi* males searched for females in and around the *nawai* territories. Moreover, to increase their copulation chances, *sahoi* males intruded repeatedly into *nawai* territories, and tried to copulate with the females ovipositing there (sneaking tactic).

In this case the mating tactics of the *nawai* and *sahoi* males were associated with the two male morphs, the orange-winged (*nawai*) and the pale orange-winged (*sahoi*). Examples of male dimorphisms associated with male mating tactics include ruff (VAN RHIJN, 1973), salmon (GROSS, 1985), beetles (EBERHARDT, 1982) and damselflies (e.g. HIGASHI, 1976; NOMAKUCHI et al., 1984; WATANABE & TAGUCHI, 1990; NOMAKUCHI et al., 1996).

NOMAKUCHI et al. (1984) observed that the non-territorial *strigata* of *M. p. pruinosa* do not fight aggressively with *esakii* males, and stated that the mating tactics of *esakii* and *strigata* males are, respectively, th territorial and sneaking

tactics. Also, UBUKATA (1979), ARAI (1982) and WATANABE & TAGUCHI (1990) observed that the territorial disputes between the orange-winged *costalis* and the hyaline-winged *ogumai* males of *M. p. costalis* were initiated only by the former, and stated that the behaviour of hyaline-winged males may be an alternative mating tactics (UBUKATA, 1979), and/or a sneaky mate securing tactics (WATANABE & TAGUCHI, 1990). It is considered, therefore, that the differences in mating tactics between two male morphs are a common feature in the Japanese *Mnais*.

On the other hand, TSUBAKI & ONO (1987) and FORSYTH & MONTGOMERIE (1987) stated that male mating tactics depends upon the age and/or body size. TSUBAKI & ONO (1987) documented that larger *Nannophya pygmaea* males occupy high-quality territories for more days than smaller individuals, and that smaller or older males occupy low-quality territories or sneak to females in or near other territories. FORSYTH & MONTGOMERIE (1987) described that some male *Calopteryx maculata* are initially territorial, but increasingly switch to sneaking as they get older.

We have no precise information on the age of individual males, but the wing lengths of *nawai* and *sahoi* were 40.3 ± 1.2 mm and 37.8 ± 1.1 mm, respectively, i.e. the mean wing length in *sahoi* was slightly smaller than in *nawai*. A difference in wing length between the two morphs was also reported in the *esakii* and *strigata* males of *M. p. pruinosa*, (NOMAKUCHI, et al., 1984). The *strigata* males were observed to aggregate and to settle around the *esakii* territories, frequented by many females, and they were able to mate frequently (NOMAKUCHI, et al., 1985). It is assumed that, due to morphological differences, the *sahoi* males are unable to occupy territories, but rather adopt an alternative mating tactics, which does not require territory maintenance but secures sneak matings at oviposition sites, instead.

REPRODUCTIVE BEHAVIOURS AND MATING SUCCESS

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 (e.g. WAAGE, 1979; MILLER & MILLER, 1981; SIVA-JOTHY, 1987). Sperm displacement in *Mnais* has recently been confirmed by SIVA-JOTHY & TSUBAKI (1989a, 1989b). Therefore, *M. nawai* males are exposed not only to competition for mates, but also to sperm competition.

The non-territorial *sahoi* males sometimes succeed in copulating with the ovipositing females in the territory of *nawai* males. In this case, the females usually continue oviposition after copulation, and the territorial *nawai* males guard them without copulation (cf. Fig. 4). Since sperm precedence has been reported in *M. p. pruinosa* (SIVA-JOTHY & TSUBAKI, 1989a, 1989b), it is suggested that these females oviposit eggs fertilized by *sahoi* males. However, when the *sahoi* males sneak to the ovipositing females and fly up in tandem off the *nawai* territory,

the female flies away without oviposition. In this case, the *sahoi* sperm may not be used for fertilizing the eggs, because these females usually oviposit after copulation with the territorial *nawai* males.

As shown in Figure 4, the territorial *nawai* males sometimes guard females without copulation. This observation suggests that most of the eggs oviposited by these females are fertilized by the sperm of *sahoi* males, i.e. these ovipositions are advantageous to *sahoi* males. Although the number of eggs oviposited by such females is not known, the total oviposition time was 185 min. On the other hand, the total oviposition time guarded by No. 152 male after copulations was 446 min. The ratio of the oviposition time of *sahoi* males to that of *nawai* males was 185/446 = 0.415. The total numbers of marked individuals of *nawai* and *sahoi* males were 131 and 50, respectively, and the ratio of the number of *sahoi* males to that of *nawai* males was 50/131 = 0.382. The values of both ratios apear to be almost equal, though the observation duration was too short to be conclusive. Therefore, the numbers of *nawai* and *sahoi* males are probably balanced by the altruistic behaviour of the former at oviposition sites.

FIELD & KELLER (1993) have reported female-mimicking behaviours as alternative mating tactics and post-copulatory mate guarding in the parasitic wasp, *Cotesia rubecula*. WATANABE & TAGUCHI (1990) stated, for the following two reasons, that the hyaline-winged males of *M. costalis* effectively mimic females in behaviour and morphology. Firstly, when the hyaline-winged male bends his abdomen to copulate, the pruinose abdominal segments 8, 9 and 10 are hidden. Consequently, the orange-winged territorial male may not recognize him as a rival, since no females are pruinose. Secondly, some orange-winged males try to form a tandem with a hyaline-winged male which was already in tandem with a female, while tandems formed by two orange-winged males were never observed. Clearly, these males appear to mistake the hyaline-winged males for females. Similar behaviour was evidenced in *M. nawai* during this study. The problems of female mimicry or female mimicking behaviour are worthy of an investigation by experimental techniques.

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