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COMPETITION FOR PERCHING SITES IN THE HYALINE-WINGED MALES OF THE DAMSELFLY *MNAIS PRUINOSA COSTALIS* SELYS THAT USE SNEAKY MATE-SECURING TACTICS (ZYGOPTERA: CALOPTERYGIDAE)

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Although hyaline-winged males of *M. p. costalis* adopt sneak tactics, the competition for occupying a perching site to intercept females entering the territory is severe. To help understand the tactic of the hyaline-winged males, their size, copulation behaviour and reproductive success were examined. The mate-securing tactics of the hyaline-winged males were divided into two. A male which succeeded in occupying a perching site was named a 'satellite', while a male which failed was called a 'wanderer'. The satellite was usually larger than the wanderer. The satellites were able to copulate with females inside the territory of an orange-winged male. The diurnal rhythm of copulations was similar for each tactic. Copulation duration was longest in wanderers outside a territory. When the duration of oviposition is used as an index of reproductive success of a male, the satellite tactic may be more advantageous than the opportunistic tactic of wanderers. However, from the viewpoint of sperm displacement, the longest copulation duration suggested complete sperm displacement by wanderers. In contrast, the relatively short copulation duration in territorial orange--winged males suggests that not all the sperm of wanderers is removed. Both the occupation of a perching site and the long copulation duration are important for the hyaline-winged males to increase their reproductive success.

INTRODUCTION

Territories are of interest in connection with sexual selection in odonates. Most of those described have involved male mating behaviour with reference to various guarding tactics for males (e.g. UEDA, 1979; KOENIG & ALBANO, 1985). Males

may remain in tandem with their mates while they oviposit or they may perch or hover by them, repelling competitor males from the area near their egg-laying mate.

In eastern Japan, *M. pruinosa costalis*, shows a wing dimorphism in males (e.g. ASAHINA, 1976). Orange-winged males usually defend territories for mating, while hyaline-winged males sneak copulation with females along the periphery of the territory (UBUKATA, 1979; SUZUKI et al., 1980; HIGASHI, 1981; NOMAKUCHI & HIGASHI, 1985; WATANABE & TAGUCHI, 1990). These latter males show two kinds of mating tactics: satellite and wanderer. The former involves perching at the periphery of the territory of orange-winged males to intercept females entering the territory. WATANABE & TAGUCHI (1990) observed a series of competitive interactions between hyaline-winged males for a suitable perching point near the territory of orange-winged males. The expelled hyaline-winged males can be observed to hold no regular perching point and are given the name 'wanderers'.

The territory occupied by orange-winged males includes substrates for oviposition. The probability of females being mated by the satellite hyaline-winged males was higher than that by the orange-winged males (WATANABE & TAGUCHI, 1990). However, the hyaline-winged males failed to fertilize the eggs, because females could be remated with orange-winged residents after mating with the hyaline-winged males. Almost 100% sperm precedence has been observed immediately after copulation in the related *M. p. pruinosa* (SIVA-JOTHY & TSUBAKI, 1989).

In this study, we compare the duration of oviposition of the females with the type of male tactic, as a measure of the hyaline-winged males reproductive success. Both tactics seem to be dependent on the territory of the orange-winged males. We firstly describe the behaviour of the hyaline-winged males and then suggest reasons for the competition for perching sites among them.

MATERIAL AND METHODS

The study was conducted along a stream (length 290 m), at an elevation of about 194 m, in the northwestern part of Kanagawa Prefecture, Japan. Width and depth of the stream were 1-1.5 m and 5--20 cm, respectively. The details of the study area have been described elsewhere (e.g. WATANABE & TAGUCHI, 1988; TAGUCHI & WATANABE, 1993).

Observations were made between 0900 and 1800, during 7 sunny days, from late May to mid June 1986. The onset of the observation period varied seasonally, corresponding to the time of peak reproductive activity of both the orange-winged and the hyaline-winged males.

During the observation period, the orange-winged males occupied 35-45 territories throughout the study area. We observed the behaviour of 29 hyaline-winged males for a whole day. The behavior of other males and females, which directly and indirectly interacted with the hyaline-winged males, in particular the sneaker males, was recorded for as long as possible.

Before the observation period (late April to late May), all the damselflies found for the first time were netted, marked individually on their hind wings with a felt-tipped pen, and then released. During the observation period in 1986, the average daily numbers in this study site (= oviposition site)

were estimated at 74, 80 and 14 for orange-winged males, hyaline-winged males and females, respectively (WATANABE & TAGUCHI, 1990).

Observations were recorded for behaviour consisting of perching, preying upon small insects, copulating, ovipositing and flying. The duration of copulation or tandem activity was recorded. Male flying patterns were recorded according to HIGASHI (1981): circle flight and dual spiral flight. The duration of oviposition posture was recorded as a measure of the number of eggs laid (e.g. WAAGE, 1978; WATANABE & TAGUCHI, 1990) and used as an index of reproductive success, because complete last male's sperm precedence for eggs laid immediately after copulation was reported in *M. p. pruinosa* (SIVA-JOTHY & TSUBAKI, 1989).

RESULTS

The orange-winged male of *Mnais pruinosa costalis* exhibited waiting mate-location behaviour. The territorial defence serve to prevent access by rival orange-winged males to sites into which receptive females entered. The orange-winged males perched on a twig or a leaf along the banks of the stream, establishing a territory.

COMPETITION AMONG HYALINE-WINGED MALES FOR SUITABLE PERCHING SITES

Hyaline-winged males arrived at the stream in the morning always later than orange-winged males. They also perched on a twig or a leaf but outside the territory of orange-winged males, and exhibited waiting mate-location behavior. There, they persisted at the perching site. When a second hyaline-winged male came and flew around the periphery of the territory, the first hyaline-winged male pursued him in a mode similar to the territorial defence showed by the resident orange-winged males towards the intruding orange-winged males. That is, the first hyaline-winged male often dashed its fore wings against the second male. Such flights included both circle flight and dual spiral flight, and usually continued for several minutes. The fighting area of the hyaline-winged males was not limited, and partly included the area of the territory of the orange-winged males. However, most or-

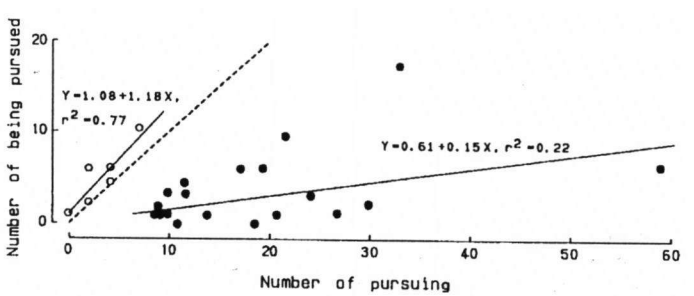

Fig. 1. Relationship between pursued and pursuing males among hyaline-winged males of *M. p. costalis* adopting different mating tactics. Filled and open circles represent satellites and wanderers, respectively. Dashed line shows the diagonal.

ange-winged males ignored them, whereas a few tried to escape from the fighting. We previously reported that the mean tracking length for hyaline-winged male was 4.2 m for 292 fights and that the maximum length was 26 m (WATANABE & TAGUCHI, 1990). None of the observed hyaline-winged males failed to defend its perching site. The defending male was named the 'satellite'. Figure 1 shows the relationship in numbers between being pursued and pursuing for each hyaline-winged male. The satellites showed much more pursuing activity to expell other hyaline-winged males from their perching sites and to adopt the sneak tactic.

The second hyaline-winged male tried to search for another perching site, which was peripheral to the territory of the orange-winged males. When a large territory of an orange-winged male was established in a topographically and vegetationally complex habitat, the periphery was so complex that we observed three hyaline--winged males perching closely to each other. However, most of these attempts usually failed, probably because, with the small territory sizes involved, there was only a single suitable perching site around the territory. When more than one hyaline--winged male were present within a complex territory, the second male moved off. However, the territory of orange-winged males was restricted along the stream, and the perching points in the periphery of these territories were already fully occupied. The expelled hyaline-winged males were usually pursued persistently by the resident hyaline-winged male wherever they went (Fig. 1). Even if such a male had arrived in an area along the stream where no territory was established, he did not stay there; no territory was established. Consequently, the hyaline-winged males that failed to get these perching sites were not site-specific throughout the day. They wandered, not along the territorial sites, but in the deciduous forest or along the forest edge to search for females, and have adopted opportunistic tactics. Such hyaline-winged males were given the name 'wanderers'.

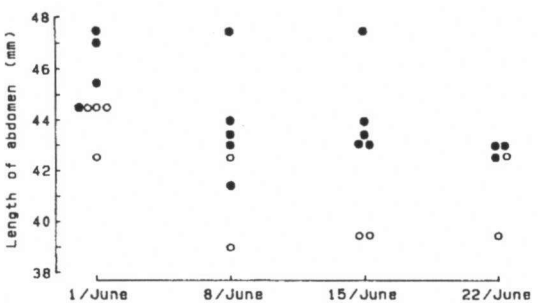

Fig. 2. Size of the hyaline-winged males of *M. p. costalis* adopting different mating tactics in each observation day, June 1986. Filled and open circles represent satellites and wanderers, respectively. There are significant differences between the two tactics on 1st ($z=1.912$, $0.05>P>0.01$), 15th ($z=2.160$, $0.05>P>0.01$) and 22nd ($z=1.793$, $0.05>P>0.01$), June, using U-test.

Figure 2 shows the data for four days that can be used to examine the size dependence of different mating tactics of hyaline-winged males. Although it can be seen that the mean size of hyaline-winged males decreased with the flight season, as in many habitats (unpublished data), the satellites were usually larger than the wanderers on each day. However, we observed that a few wanderers showed satellite behaviour on subsequent days.

Table I

The proportion of females copulating with hyaline-winged males that adopted different mating tactics in the territory of orange-winged males

Copulation partner	Number of males observed	Number of copulations observed	Number of copulations in territory	Proportion of copulations in territory (%)
Satellite	20	74	43	58.1*
Wanderer	9	7	1	14.3*

*: $P<0.05$ (χ^2-test)

MATING BEHAVIOUR AND MATING SUCCESS

The number of suitable perching sites for hyaline-winged males was limited. Because the flight trajectories of females entering territories seemed to be stable for each territory, the satellites were able to sneak in at the periphery of the territories established by the orange-winged males. On the other hand, for the wanderers, their opportunistic mating tactics did not increase the number of observations on courtship behavior and copulation. They tried to mate wherever they encountered a female.

As shown in Table I, we observed throughout one day 29 hyaline-winged males (20 satellites and 9 wanderers). All satellites had more than one copulation (mean 3.7), while 5 out of 9 wanderers failed during the observation day (mean 0.8). Most hyaline-winged males formed tandems without any courtship behaviour immediately after the encounter. More than half of the copulations involving satellite males were observed inside the territory of the orange-winged males. The wanderers were not able to enter the territory as the satellites did. This suggests that a satellite can easily enter the territory without harassment by the orange-winged male.

The frequency of copulations for hyaline-winged males was low in the morning and increased during the day (Tab. II). Although we do not know how often the wanderers copulated far from the water (i.e. out of our area of observation), the hyaline-winged males seemed to have a similar diurnal copulation rhythm, irrespective of their mating tactic.

Due to the opportunistic tactics of wanderers, we were able to measure the duration of copulation in only six cases. As shown in Table III, it is clear that the duration of copulation outside the territory was longer than that

Table II

Copulation frequency for hyaline-winged males adopting different mating tactics (number/hour/male)

Copulation partner	0900 - 1200	1200 - 1500	1500 - 1800
Satellite	0.4±0.1 (37)	0.6±0.1 (57)	0.8±0.1 (39)
Wanderer	0.1±0.1 (13)	0.5±0.3 (10)	0.7±0.3 (3)

( ): Number of males observed

Table III

Copulation duration for hyaline-winged males adopting different mating tactics in each copulation site (sec±SE)

Copulation partner	Inside of territory	Outside of territory	
Satellite	69.8±4.1 (34)	105.8+ 8.1* (32)	Z=4.064, P<0.01
Wanderer	74 (1)	139.2+11.8* (5)	—

*: Z=1.978, 0.05>P>0.01 (Mann-Whitney U-test)
( ): Number of pairs observed

within the territory for both satellites and wanderers. Copulation within the territory always has a risk of interruption by an orange-winged male attack. In fact, three out of 34 copulations with satellites were harrassed by the territory owners. It might also be necessary for a satellite to return quickly to his original perching site, since the vacant perching point was easily occupied by wanderers. In consequence, the copulation duration inside the territory tended to be shortened.

The wanderers might take much more time to copulate than the satellites, because there might be no harassment by other males. Few of them copulated near territories or by satelite perching sites. After mating with wanderers, many females are likely to remate with other males when they enter a territory to oviposit. However, the wanderers do retain some mating success, because sperm displacement was sometimes incomplete due to the short second copulation duration (cf. WATANABE & TAGUCHI, 1990), and because the wanderers thoroughly complete sperm displacement during copulation.

The total duration of oviposition posture was measured for each female which copulated with hyaline-winged males adopting different mating tactics. About one third of the females that copulated with hyaline-winged males re-copulated with the territorial orange-winged males. The eggs deposited by such females may be inseminated by the last males' sperm. Table IV shows the duration of oviposition posture of females without recopulation by orange-winged males. The mating success of satellites increased in the evening, since an excess number of females tried to enter the territories for oviposition. The orange-winged males were unable to copulate with all of the females. However, no females that mated with wanderers oviposited, since most of them remated either with the satellites or with the orange-winged males before they started to oviposit. A few of them flew out of the study area.

Table IV

Duration of oviposition posture for females after copulation with hyaline-winged males adopting different mating tactics until remating or flying away (min/h/male)

Copulation partner	0900 - 1200	1200 - 1500	1500 - 1800
Satellite	1.8±1.0 (37)	5.1±1.6 (57)	8.2±2.8 (39)
Wanderer	0.0±0.0 (13)	0.0±0.0 (10)	0.0±0.0 (3)

( ): Number of females observed

DISCUSSION

For typical orange-winged males of *Mnais pruinosa costalis*, the territory includes a settling base from which the occupant surveys the territory, makes sallies towards intruders and embarks on intermittent patrol flights (e.g. HIGASHI, 1981; NOMAKUCHI, 1988; WATANABE & TAGUCHI, 1990). Since it also includes the oviposition site, the males have to arrive at the area earlier in the day than females, and establish a territory before the females arrive. Males then try to copulate with the arriving females.The hyaline-winged males, on the other hand, do not use territorial tactics, though NOMAKUCHI et al. (1984) reported that they held a territory when all of the orange-winged males were removed. In our study area, the hyaline-winged males also arrived at the oviposition area later in the day than the orange-winged males and occupied a suitable perching site to sneak females at the periphery of the territory.

Aggressive behaviour exhibited by the hyaline-winged males at the perching site was directed mostly towards other hyaline-winged males, which consequently became wanderers. CORBET (1980) stated that the nature and intensity of aggressive behavior vary within species in accordance with the male density or the distance from the centre of the territory. However, the limited number of perching sites elicited much more severe competition for territory among the hyaline-winged males than among the orange-winged males. Although the perching site is dependent upon quantity and quality of the territory of orange-winged males, the competition for a perching site seemed to be similar to that for a territory of orange--winged males. Therefore, the perching site is important for hyaline-winged males to increase their reproductive success.

Especially when sperm displacement occurs during copulation (e.g. WAAGE, 1979; SIVA-JOTHY & TSUBAKI, 1989), reproductive success clearly results in strong sexual selection in favour of those orange-winged males that are able to maintain a territory. Most females that copulated with a territorial orange-winged male began to oviposit within his territory. WATANABE & TAGUCHI (1990) showed low reproductive success in some orange-winged males that failed to establish a territory, named 'floaters'. The hyaline-winged males were willing to perch at the periphery of a territory, where they tried to intercept arriving females. Such sneak tactics in satellites has been reported previously (e.g. UBUKATA, 1979).

For a hyaline-winged male, the risk of take-over is great and guarding is inopportune, because their mates have to enter the territory to oviposit. Therefore, the hyaline-winged males do not guard females, and their reproductive success might be low. However, the territorial orange-winged males often guarded one or more mates, including females last inseminated by the hyaline-winged males. WATANABE & TAGUCHI (1990) suggested that this might be the result of confusion of the males, as that satellites seem to mimic the females in behaviour and in morphology. In this study, about two thirds of the females that copulated with

satellites oviposited without recopulating with the territorial orange-winged males. Consequently, their reproductive success depends on the ability of their mates to exploit the guarding behaviour of the orange-winged males without copulation.

Our assessment of the reproductive success of the wanderer may be underestimated. Because wanderers usually stayed in the deciduous forests or on the edges thereof, it was difficult to completely observe their behaviours. WATANABE (1991) pointed out that hyaline-winged damselflies preferred sunflecks in deciduous forests. It is clear that when a wanderer encounters a mate the copulation duration is long and sperm displacement probably complete. However, most females that copulated with wanderers recopulated with orange-winged males at the oviposition site. There, sperm displacement might occur again. Since the copulation duration of territorial orange-winged males lasts for about one minute (WATANABE & TAGUCHI, 1990), there is a possibility that not all the sperm of wanderers is removed.

The wing colour dimorphism in *Mnais* has been interpreted in terms of different mating tactics (e.g. UBUKATA, 1979; NOMAKUCHI et al., 1988). While CORBET (1980) reviewed the behaviour of non-territorial males, including the sneaking tactics, so far no suggestion has been made to the effect that the sneaking tactic itself is the result of competition among the non-territorial males. In the present study, we have outlined the competition for perching site and its consequences for reproductive success in the hyaline-winged males. Additional studies on female behaviour may elucidate the relative importance of the male mating tactics in male wing dimorphism in this species.

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