

**BEHAVIOURAL PROTANDRY IN THE DAMSELFLY
MNAIS PRUINOSA COSTALIS SELYS
IN RELATION TO TERRITORIAL BEHAVIOUR
(ZYGOPTERA: CALOPTERYGIDAE)**

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The reproductive strategy of the male *M. p. costalis* can be defined as an attempt to maximize the number of females mated. Males exhibit wing colour dimorphism: one form has orange wings, and the other has hyaline wings which resemble female wings. The former is usually territorial and the latter uses sneaky mate securing tactics around the territories of orange-winged males. Although the length of the emergence period varied from year to year, no evidence of protandry was observed. Studies over 10 years have shown that if the length of the sexually active period in females is stable, the orange-winged males should become sexually mature before females do to achieve maximal reproductive success. On the other hand, the hyaline-winged males do not mature before females due to the fact that they utilize the territories of orange-winged males. This study shows that behavioural protandry should be considered a reproductive strategy of the orange-winged males for establishing territories.

INTRODUCTION

In most insect having non-overlapping generations males emerge before females. This is known as protandry. Theories on protandry have been developed in terms of sexual selection acting either on males to maximize the expected number of matings (IWASA et al., 1983), or on females to minimize the prereproductive period (BULMER, 1983). However, WIKLUND & FAGERSTROM (1977) advance the hypothesis that protandry is the optimal reproductive strategy of males, particularly in species maintaining female monandry. The protandry theory also focusses on species in which generations are discrete (e.g. SINGER, 1982). As might be expected, due to the polyandrous nature of female odonates,

protandry in respect to emergence is found only in a few species (CORBET, 1999).

Although protandry can be a mutually optimal reproductive strategy for both sexes, the benefits of protandry may be different for each. In species where the adults of both sexes emerge during a limited period and where the females are polyandrous, as in the case of *Mnais pruinosa costalis*, a male's chances to reproduce are usually restricted to the comparatively small area in which the female will oviposit. Therefore, males must establish territories nearby. However, each damselfly needs a period of about 1 week before reaching sexual maturity (e.g. WATANABE, 1991). We expect males to be more likely than females to adjust their maturity in order to maintain protandry. We might also expect lower variance in eclosion time in males than in females (PARKER & COURTNEY, 1983). Our analysis is based on the assumption that males are selected by their ability to maximize the number of females they mate with. It is also assumed that males compete intraspecifically for females to mate with.

The males of *M. p. costalis* are dimorphic in wing colour: orange-winged males usually defend territories for mating (WATANABE & TAGUCHI, 1990), while hyaline-winged males sneak in to copulate with females along the periphery of the territory, while the orange-winged male is off defending his perching site (WATANABE & TAGUCHI, 1997). When analyzing the issue of protandry, the two different mating strategies must be taken into account. Because the perching sites of hyaline-winged males are located around the periphery of the orange-winged males territory, the chance to reproduce for the hyaline-winged males is dependent on the establishment of territories by orange-winged males. Consequently, the hyaline-winged males need to mature after orange-winged males, and there must be little protandry in the hyaline-winged males.

MATERIAL AND METHODS

The study area for *M. p. costalis* was located in the northwest section of Kanagawa Prefecture. By using mark and recapture methods, TAGUCHI & WATANABE (1992) showed that the habitat of this species is very isolated, and that little immigration or emigration was occurring. This area is very hilly and covered with deciduous forests. The study sections were located along an open stream, which is 1-2 m wide. In summer, the stream became more heavily covered due to branches and shrubs growing out and over the water. A detailed description of the study area can be found elsewhere (WATANABE & TAGUCHI, 1988; TAGUCHI & WATANABE, 1993).

For a 10-year period (1980-1989), surveys were conducted from the onset of emergence (middle April) to the end of the adult flight season (late July). Although the onset of the emergence period varied from year to year, the total number of sampling days each year was 15. Sampling was conducted on those days that the weather was clear. The study site was 550 m long including an upriver section of a tributary to the main stream.

During 1981-1985, censuses of adults were taken along the stream three times a day: morning (09:00-10:30), noon (12:00-13:30) and afternoon (14:30-16:00) every week. For 5 years (1980 and 1986-1989), censuses were taken only once around 12:00. During each sampling period, we patrolled the streams and the paths in the neighbouring forests. All of the damselflies found were captured by net, and then marked individually on their hind wings. The sex, degree of sexual maturity (cf. WATA-

NABE & TAGUCHI, 1990, 1997), abdomen length, hind wing length and the wing form were recorded for each individual. Then, they were released. The marking was considered to have only minor effects on flight activities (and the probability of mating) because most damselflies began to fly and perch normally soon after release. Damselflies wounded during marking were treated as dead individuals in the calculations. This mark and recapture method is nearly the same as the one that WATANABE et al. (1998) have used. Since the recapture probabilities among orange-winged males, hyaline-winged males and females are different due to their behaviours (WATANABE & TAGUCHI, 1990, 1997), the sexes and male wing forms of *M. pruinosa* were processed separately through an analysis such as Jolly's model (JOLLY, 1965) or similar methods.

The sexually mature males were distinguished from immatures by the extent of palely pruinosed abdomen (orange-winged: all abdominal segments, hyaline-winged males: abdominal segments s1-3 and s8-9). The dorsal abdomen of mature males changed from green to smoky metallic green because of heavy pruinescence, and the pterostigma colour changed from white to red. Additionally, the sexually mature females had no pruinosity on the dorsal abdomen or white pterostigmata. Mature females were identified by the degree of the pruinescence on the thorax and their wing condition. The tips of the abdomens were also examined in order to determine if they had oviposited.

RESULTS

When *M. p. costalis* emerged from the stream, it immediately moved into the neighbouring deciduous forests and stayed there while sexually immature. Table I shows similar patterns in daily number of immature damselflies for both male morphs and females found in the stream over the 10-year period. Since most immature individuals having emerged that day were teneral, Table I roughly represents the emergence pattern for each male morph and for females. The emergence was nearly synchronous among the two male morphs and for females, though the yearly size of those populations varied considerably. During the course of the 10-year survey period, the earliest record of initial emergence date was April 24 (1983) and the latest record was May 6 (1984). The average date at which new emergence ceased was in early June for orange-winged males, and in late June for hyaline-winged males and females. The emergence period of the orange-winged male was the shortest of the three.

Imagoes matured sexually about 10 days after emergence. Most of them returned to the original stream that they emerged from. Males exhibited various mating tactics there, such as territorial behaviour, sneaky behaviour, and so on. Conversely, females remained in the forests for the most part, making short visits to the stream in order to oviposit.

As shown in Figure 1, we found a few mature orange-winged males and hyaline-winged males, and a few females at the stream on the same day that they matured. In all 10 years, the appearance of mature orange-winged males at the stream was sooner than that of the hyaline-winged males. Although many mature females were not observed due to their brief visits to the stream site, the peak date in their maturity was at or after the end of May. Consequently, the peak population for each of the 2 male morphs and for females was observed on a different date.

Table I
The number of immature *Mnais pruinosa costalis* found in the stream (No./day)

		Apr		May		June			July		Aug	
		late	early	mid	late	early	mid	late	early	mid	late	early
1980	Orange	0	0	1	0	0	0	0	0	0	0	0
	Hyaline	0	1	2	3	1	0	0	0	0	0	0
	Female	0	5	1	0	1	0	0	0	0	0	0
1981	Orange	0	26	12	3	2	0	0	0	0	0	0
	Hyaline	0	24	13	5	5	3	4	0	1	0	0
	Female	0	36	16	10	3	3	4	1	0	0	0
1982	Orange	2	33	4	1	0	0	0	0	0	0	0
	Hyaline	1	39	17	3	9	2	1	1	0	0	0
	Female	10	65	8	3	2	0	1	0	0	0	0
1983	Orange	5	33	2	2	0	0	0	0	0	0	0
	Hyaline	9	39	5	5	5	0	0	0	0	0	0
	Female	17	54	2	3	3	1	0	0	0	0	0
1984	Orange	0	11	0	29	0	4	3	0	0	0	0
	Hyaline	0	18	0	23	3	9	3	1	0	0	0
	Female	0	26	0	20	2	4	5	2	0	0	0
1985	Orange	2	14	7	2	2	0	0	1	0	0	0
	Hyaline	4	20	6	2	2	1	0	0	0	0	0
	Female	1	15	11	2	4	4	2	0	0	0	0
1986	Orange	1	5	5	3	0	0	0	0	0	0	0
	Hyaline	0	4	4	3	1	0	0	1	0	0	0
	Female	2	8	4	3	1	0	1	1	0	0	0
1987	Orange	0	11	6	0	0	0	0	0	0	0	0
	Hyaline	0	6	2	0	0	0	0	0	0	0	0
	Female	0	19	3	1	0	0	0	0	0	0	0
1988	Orange	0	56	0	4	0	0	0	0	0	0	0
	Hyaline	0	58	1	5	1	1	1	0	0	0	0
	Female	1	104	2	11	2	0	2	0	0	0	0
1989	Orange	23	14	27	8	6	0	0	1	0	0	0
	Hyaline	24	3	25	16	11	3	4	1	0	0	0
	Female	36	11	14	9	2	0	3	2	0	1	0

The total number of individuals marked in each year is shown in Table II. Although the number of orange-winged males marked was lower than hyaline-winged males, the recapture rate of orange-winged males was higher than that of hyaline-winged males due to their reproductive tactics. Most orange-winged males stayed near the study stream in order to establish territory, while hyaline-winged males wandered along the stream as well as in the nearby forests. Females also had lower recapture rates than the orange-winged males because of their short visits to the stream. Consequently, each SD for the estimated daily number of orange-winged males was the smallest, calculated using Jolly's model (JOLLY, 1965). The estimated daily numbers of orange-winged males, hyaline-winged males and females were less than 100, around 150, and around 250,

respectively in the peak flying period of each year, suggesting that the sex ratio of *M. pruinosa* was equal.

As expected under the assumption that protandry mirrors mating strategy, the orange-winged individuals that visited the stream sooner to establish territories were those that developed into mature adults first. We also compared the data to determine if orange-winged males, hyaline-winged males, or females were the first to arrive at the stream. It appears that orange-winged males arrive sooner than females (Fig. 2).

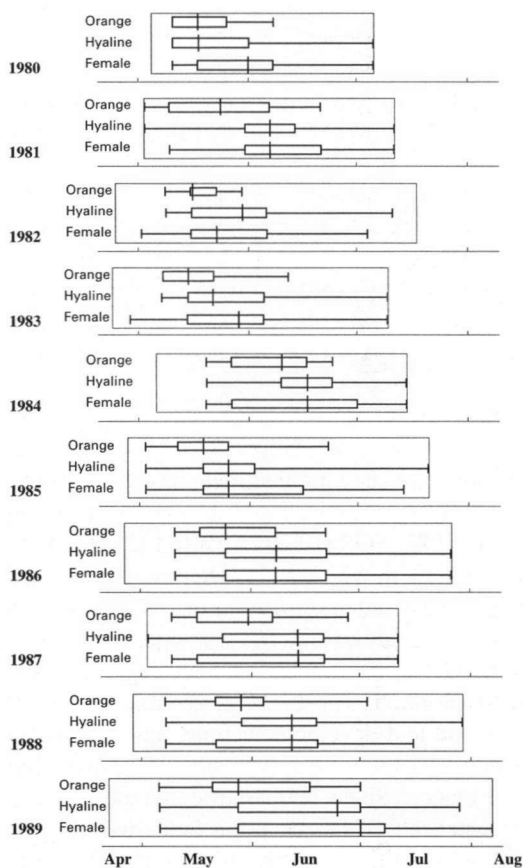


Fig. 1. Day of first observation of sexually mature individuals in orange-winged males, hyaline-winged males and females. – [The box with the centre line represents interquartiles and the median day. The bars indicate the range of the earliest and the latest days that mature individuals were observed. The dotted area shows the flight season of *M. p. costalis* in each year].

In all 10 years, it appears that the peak emergence time, as well as maturity rates in adults were different between orange-winged males and females in agreement with the hypothesis. However, the hyaline-winged males started to mature at the same time as females. The approximate diagonal could be interpreted as a tendency for no time lag in hyaline-winged males occurring at the beginning of the season, followed by females. This might lead to a hypothesis that the numbers of sneaker males will never exceed the number of territorial males. Therefore, protandry should be a reproductive strategy found in orange-winged males and not in hyaline-winged males.

Table II
The number of *Mnais pruinosa costalis* marked during the flying season and the estimated daily number of damselflies at the peak flying activity period calculated by Jolly's model

Year	The number of marked individuals			The estimated daily number		
	Males		Females	Males		Females
	Orange	Hyaline		Orange	Hyaline	
1980	43	130	104	98 ± 107	223 ± 124	307 ± 310
1981	102	370	321	39 ± 7	184 ± 18	264 ± 98
1982	129	341	414	57 ± 12	106 ± 16	260 ± 138
1983	139	331	357	62 ± 7	256 ± 164	687 ± 548
1984	131	318	216	40 ± 9	148 ± 24	204 ± 152
1985	70	183	129	23 ± 35	129 ± 150	88 ± 89
1986	60	158	95	59 ± 74	108 ± 160	60 ± 76
1987	54	140	59	253 ± 302	123 ± 77	115 ± 307
1988	243	375	337	134 ± 38	302 ± 200	272 ± 313
1989	148	356	226	83 ± 41	146 ± 79	113 ± 143

DISCUSSION

There are many examples in the literature showing that male insects are apt to contribute to the maintenance of protandry through rapid development during their larval stages (e.g. IWASA et al., 1983; FORSBERG & WIKLUND, 1988). Protandry can be seen as a mating strategy in which males attempt to maximize their number of copulations, while females attempt to minimize the time they spend mating. However, in most odonate species, neither sex emerges earlier (e.g. TROTTIER, 1966; SAWCHYN & GILLOTT, 1975; UTZERI et al., 1988; CARON & PILON, 1990; BEFELD et al., 1997). In *M. p. costalis* the emergence date depends on oviposition date and development time, and few males emerge before the females. This suggests that males typically do not develop faster than females in their larval stages. Since temperature fluctuations are partly unpredictable, the developmental rate of larvae in the fields will also be unpredictable from year to year. However, the spring species (CORBET, 1962) including *M. p. costalis* tend to have a synchronized emergence period of short duration (NOMAKUCHI et al., 1988). Typically the variance in eclosion times is assumed to be caused by environmental unpredictability. The two male morphs and the female populations emerge according to given time curves of eclosion which are under genetic control respectively.

Considering that polyandrous females have no restraints placed upon them by males against subsequent matings, it can be assumed that there is no strong selection for protandry in these species. Females are receptive for mating at the oviposition sites as well as the roosting sites after a certain period of sexual immaturity.

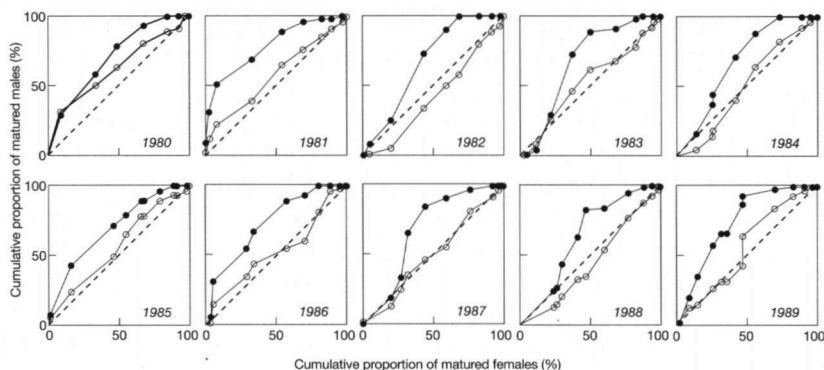


Fig. 2. Cumulative percentage curves of mature orange-winged males (closed circles) and mature hyaline-winged males (open circles) in relation to that of mature females. – [The broken line represents a diagonal which shows the same maturity curve between each male type and female. See Tab. I for the total number of orange-winged males, hyaline-winged males and females in each year].

However, there appears to be less chance for males to find acceptable females in the forest, compared to the chance of finding a female if they have territory at the stream. Some hyaline-winged males tend to adopt the former mating tactic while orange-winged males adopt the latter tactic (WATANABE & TAGUCHI, 1990, 1997). Therefore, orange-winged males need to arrive at the oviposition site before females. Although we do not present quantitative data for the duration of the immature stage in each male morph and in females, the emergence pattern suggests that orange-winged males have a shorter period of sexual inactivity as adults. In general, females are heavier than males, as a result of more strongly mass-dependent reproductive success in females than in males. There are many odonate species in which the duration of immature stages of females considerably exceeds that of males (e.g. FINCKE, 1986; HINNEKINT, 1987; BENNETT & MILL, 1995).

The maturity patterns in Figure 1 represent all 10 years with an average difference in time to maturity for the two male morphs and females. It is in marked contrast to the emergence pattern as shown in Table I. The variability of the maturity patterns found here is caused by two things. Firstly, the number of damselflies sampled each year varied, partly due to a one-week sampling period. Secondly, temperature fluctuations during the emergence and immature stage periods caused an irregular pattern in emergence distributions for each of the years. HIGASHI (1982) did not find any difference in the length of immature stages between the two male morphs of *M. p. pruinosa*.

Because selection for protandry is strongest in species where females are monogamous (e.g. FAGERSTROM & WIKLUND, 1982), it might be less important in species with an increased degree of female polyandry. According to the so-called

sperm competition hypothesis, males that produce a large ejaculate are expected to fertilize more eggs than males producing a smaller one. This because they induce a delay in the secondary matings of the female (e.g. BOGGS, 1981). If this is true, sexual selection will favour large ejaculates and, indirectly, large male size. However, from the viewpoint of sperm displacement in Odonata (e.g. WAAGE, 1979), where there is no delay in second matings of females, protandry must be explained as the result of the competition for lifetime mating frequency. For females, the number of matings is not a limiting factor in reproductive success because females store sperm. Nearly all females mate every time they return to oviposition sites, and many remate between bouts of oviposition in the same clutch. Therefore, odonate female polyandry does not affect protandry. There are only a few reports quantitatively showing protandry in which males emerge earlier than females, such as *Tetragoneuria cynosura* and *Gomphus exilis* (LUTZ & McMAHAN, 1973) and *Aeshna umbrosa* (HALVERSON, 1984).

Both orange-winged and hyaline-winged males of *M. p. costalis* seem to use a mating tactic dependent upon varying arrival time to the stream. The frequency of successful copulations lies in the establishment of territories for orange-winged males which will then have more opportunities to mate. This means that the fitness of the males maturing earlier is higher than that of males maturing later. On the other hand, because the perching sites used by hyaline-winged males to sneak females are located near the territories of orange-winged males (WATANABE & TAGUCHI, 1997), it is not necessary for the hyaline-winged males to mature earlier than orange-winged males. Less protandry in hyaline-winged males could be explained by use of the sneaky mating tactics. In addition, the decreased encounter rate in the case of hyaline-winged males adopting opportunistic tactics in the forests makes selection for protandry less intense (e.g. ZONNENVELD & METZ, 1991). Therefore, the selective pressure on orange-winged males is stronger than that on hyaline-winged males. Protandry in damselflies is a reproductive strategy of the male, resulting from competition for mates, particularly in orange-winged males trying to establish territories. Although males and females have different reproductive strategies, males selected to maximize their overall copulatory numbers and females to minimize the time lag between mating and oviposition, both work in the same direction. In conclusion, we consider that our paper has shown that protandry is beneficial to males trying to establish territories, and provides a basis necessary for understanding behavioural protandry as an evolutionarily stable strategy in damselflies.

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