

**DIURNAL CHANGES IN PERCHING SITES AND LOW MOBILITY
OF ADULT *MORTONAGRION HIROSEI* ASAHINA
INHABITING UNDERSTORY OF DENSE REED COMMUNITY
(ZYGOPTERA: COENAGRIONIDAE)**

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Shifts between perching sites, the flying behaviour as well as reproductive behaviour of adults were observed. All marked individuals inhabiting the dense reed community floor were followed from sunrise to sunset. Simultaneous observation was carried out by approximately 20 researchers. Every adult, sexually immature and mature, perched at 20 cm above the water surface within the reed community. For immature adults, about 120 flight activities were performed per day. The accumulated length of the movement was 9 m per day. When matured, the number of flight activities increased two-fold and the total length of the movement was 27 m per day. Although this sp. is a percher, showing little movement, increased flight activity by mature individuals caused encounters between individuals, hovering face-to-face. Few tandem flights were observed and ♀♀ oviposited alone. The behaviour traits of this sp. at low light intensity are discussed.

INTRODUCTION

Perching behaviour in relation to the sit-and-wait tactic for feeding, mating, and so on has been documented for many odonate species termed "perchers" by CORBET (1999). Species whose males establish territory without continuous patrol flights are also considered to be perchers. In most cases perching sites allow the dragonfly an open view of its surroundings, except when roosting or escaping from predators. However, some species such as *Platycnemis echigoana* requires the understory of forests where the visibility must be extremely unfavourable, and therefore they exploit sunflecks for rendezvous (WATANABE et al., 1987). Consequently, species inhabiting forests generally concentrate in sunlit areas including forest gaps (KIRKTON & SCHULTZ, 2001; WATANABE et al., 2004) or sunflecks (WATANABE & MATSUNAMI, 1990). Sexually immature adults of many species also prefer to enter forests (SAWCHYN & GILLOTT, 1974;

BENNETT & MILL, 1995) and perch to roost and forage throughout the day.

Among odonate species, the absence of dispersal pertaining to maiden flights in *Mortonagrion hirosei*, that inhabits the understory of dense reed communities in brackish water or estuaries (WATANABE & MIMURA, 2003), must constitute a particular characteristic of their movement behaviour because few of them disperse from the reed community from which they emerge. WATANABE et al. (2002) reported that the relative light intensity in most of their perching sites was less than 10%, and concluded that the physical environment of the understory of dense reed communities was comparable with that of the forest floor. After emergence, *M. hirosei* adults remain in the understory of the reed community throughout their life span showing little flight activity, where they express reproductive behaviour when sexually mature (HIROSE & KOSUGE, 1973; SOMEYA, 1998; FUKUI & KATO, 1999). However, little attention has been paid to the perching behaviour of *M. hirosei*, probably due to the damselflies' cryptic colouring inside the understory of dense reed communities. In addition, it is difficult to identify adults, due to their species' specific small body and little flight activities.

The aim of the present study was to obtain quantitative information regarding the diurnal perching behaviour of *M. hirosei* adults. We used a marking technique to identify the flights of each individual, and to allow each perching site to be easily identified in the reed community. We also observed the interaction among adults, which should help to clarify the *M. hirosei* mating system.

STUDY AREA AND METHODS

In Ise City, Mie Prefecture, Japan, there remain still many reed communities established on the brackish water in estuaries, but *M. hirosei* has been found in only a few reed communities located far apart from each other. Therefore, each habitat of *M. hirosei* was thoroughly isolated. Their present habitat consists mainly of very slow-flowing streams with muddy bottoms flowing into fresh water from sewage and saline water from the sea (50 m long, 10 m wide). The water depth was less than 10 cm in pure dense communities of the reed *Phragmites communis* which produces a shady understory for the community. The mean density of 440 live and withered reed stems per square metre corresponds to a mean distance of approximately 5 cm between reed stems. No reeds were trimmed in 2000 and 2001, and the community was about 2–2.5 m tall during the present study. No pesticide was used on the paddy fields during the flight season. To the east, the stream continues to Ise-Bay and the sea.

Adults of *M. hirosei* were found in the reed community from late May to early August. Before the observation of adult behaviour, they were captured with a net and anaesthetised using CO₂, and each was then marked with its own number on the undersurface of the left hind wing using a black felt-tipped pen and released. The marking was considered to have only minor effects on their flight activities (and the probability of mating), since most damselflies began to fly normally and then perch soon after emerging from the anaesthetic.

Although in the present study the age of each damselfly was estimated according to seven classes, mainly by wing condition and body colours (WATANABE & MIMURA, 2003), each adult was placed in either of three categories, namely, "teneral" for those on the day that they emerge, "immature adult" for those in the pre-reproductive period and "mature adult" for those in the reproductive period.

The observation day corresponded to the time of peak population density of *M. hirosei* (estimated daily adult population was ca. 1,000, i.e., 2 adults per square metre), in late June (WATANABE & MIMURA, 2003), which is a monsoon season in Japan. Observations were then made in the intermissions between rains and for mostly sunny days in both 2000 and 2001. About 20 researchers were employed to simultaneously observe

the behaviour of the marked adults in both immature and mature stages for entire days in both years.

Marked adults were continuously followed for as long as possible throughout the day: from sunrise (0500) to sunset (1930), monitoring the time spent performing various behaviours. We recorded behaviour consisting of perching, preying upon small insects, copulating, ovipositing, and flying in immature and mature adults. The distance of each flight and the height of perching site were also recorded. Flight behaviour was divided into two types in accordance with the flight route: shift flight and interrupted flight. The former was the movement directly from one perch to another. The latter was an interrupted shift flight in which the individual returned to its original perch for no observable reason (as determined by the observers). This type of flight was not for aimed at feeding and was not directed to any other detectable insects. Encounter flights were easily identified, being caused by interference from other *M. hirosei* adults coming near the perch, mainly resulting in so-called face-to-face hovering. In every flight behaviour, the duration was less than 1 sec, as in the case of *Platycnemis echigoana* (WATANABE et al., 1987) and *Lestes sponsa* (WATANABE & MATSUNAMI, 1990). The total number of adults observed continuously for more than 5 min were 20 and 22 immature males and females, and 64 and 16 mature males and females, respectively, over the two years.

RESULTS

In each observation day, the adult population structure was very heterogeneous with respect to age distribution. We found a few teneral, some immatures and matures. Aged females were ovipositing on the same day. Both immature and mature adults tended to remain throughout the understory of the reed community, though there were patchily some patches of dry area unsuitable for oviposition on the community floor. Individuals perched mainly on both the live and withered stems of reeds, preferring the tip of broken shoots and broken blades of reeds. The height of the perching site for each sex and/or each maturation stage was ca. 20 cm above the water or ground surface throughout the

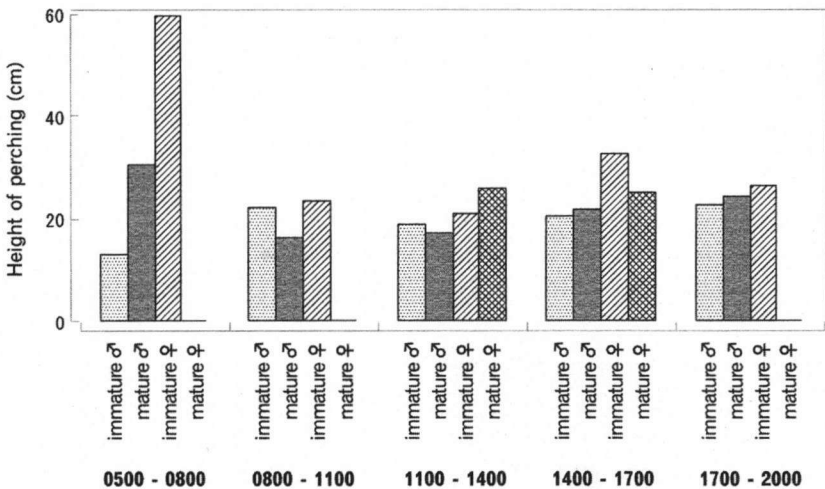


Fig. 1. Diurnal changes in the height of perching sites above the water's surface within the reed community for *M. hirosei* at immature and mature stages. Each height is the sum of individuals calculated with length of the duration of perching.

day, except in the early morning (Fig. 1). We found some adults roosting at relatively high perching sites in the margin of the community during the night, but most of them entered the community after sunrise.

There was no diurnal change in the frequency of shift flights for perching sites in immature adults (Fig. 2). The number of shifts per hour was about 3-6 for both males and females. They took place irregularly and there was no diurnal tendency regarding intervals between the shift flights. The number of shift flights of mature males in either early morning or evening was about 4 per hour, which was not significantly different from that of immature males. Around noon, however, the number of shift flights of mature males significantly increased to about twice of that of immature males. On the other hand, the number of shift flights of mature females was not significantly different from that of immature ones.

Each distance of shift flight by immature males was around 15 cm without diurnal change. Immature females also showed short distance shift flights that were slightly longer than those of immature males, though there were no significant differences be-

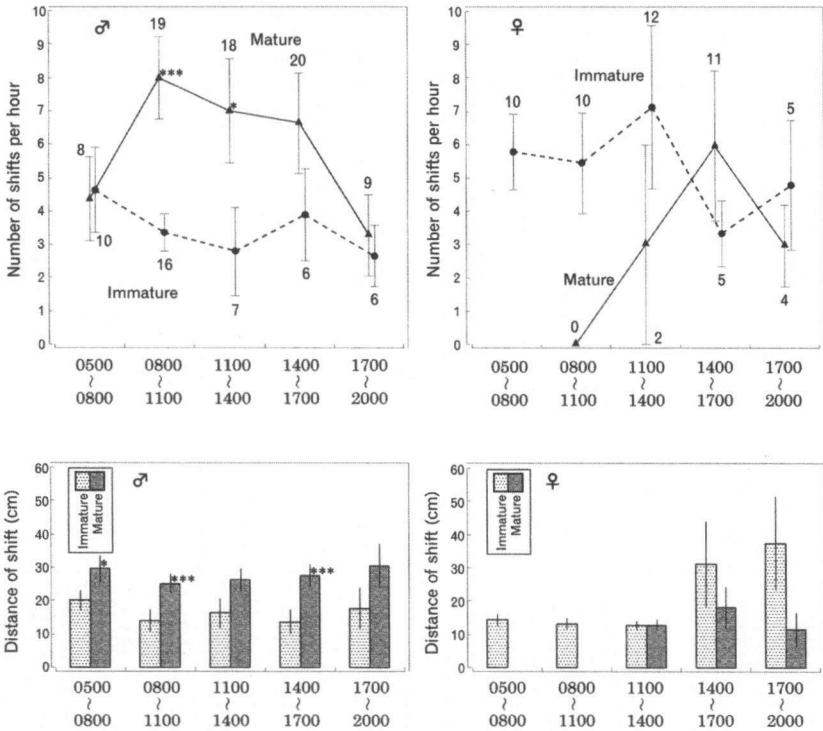


Fig. 2. Diurnal changes in the number and the distance of the shift flight of *M. hirosei* at immature and mature stages. Each bar represents SE. The numbers above the symbols show sample size during the three-hour measurement period. * and *** indicate significantly higher values in mature than in immature adults at a probability of less than 0.05 and 0.01, respectively (Mann-Whitney U-test).

tween two. When the males matured, each shift flight distance was significantly longer (ca 30 cm) than that of immature males. Although the number of mature females observed was small, the distances of their shift flights were not significantly different from those of immature females.

The frequency of interrupted flights varied among individuals, irrespective of the maturation stages and sexes. One adult showed few interrupted flights throughout the day and the other made many flights. About 4 interrupted flights per hour in the morning was the highest activity recorded throughout the day for immature and mature males (Fig. 3). No trend was observed regarding the frequency of interrupted flights, though the number of interrupted flights of mature males was significantly higher than that of immature males in the evening. The frequency of interrupted flights by immature females particularly showed a high level of activity in the early morning. There was no relation between shifting and interrupted flights in each maturation stage and each sex. The destination on the wing during a single interrupted flight was short, and the distance was about 10-15 cm for either sex and for either maturation stage.

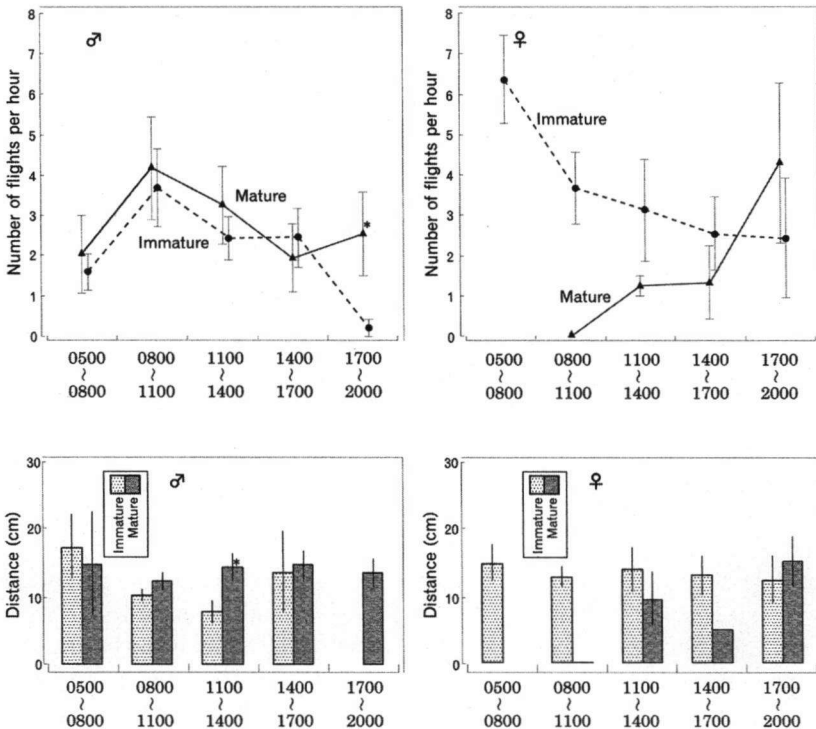


Fig. 3. Diurnal changes in the number and the distance of the interrupted flight of *M. hirosei* at immature and mature stages. Each bar represents SE. Each sample size during the three-hour measurement period is shown in Fig. 2.

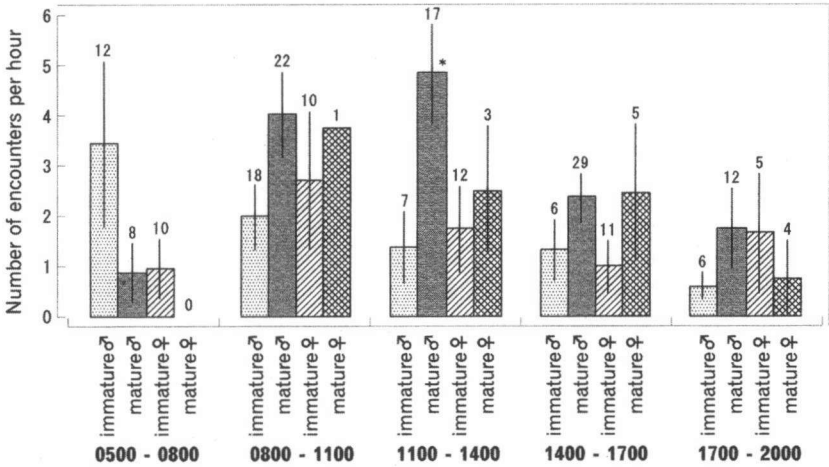


Fig. 4. Diurnal changes in the number of encounters of *M. hirosei* at immature and mature stages. Each bar represents SE. The numbers above the symbols show sample size during the three-hours measurement period. * indicates significantly higher values in mature than in immature adults at a probability of less than 0.05 (Mann-Whitney U-test).

Encounters between or among adults were observed whenever they tried to perch close to one another. Since most of them perched throughout the day, the encounters occurred just after the shift flight of other individuals regardless of sex and maturation stages. Consequently, the frequency of encounters seemed to depend on the frequency of the shift flights. A continual wing-spreading display by perching females as a refusal response to a courting male was observed during the encounter behaviour. Physical contact among the adults was never noted. Whenever adults encountered each other, they hovered at face-to-face within 1-3 cm of one another for a couple of seconds, appearing to mirror each other's hovering behaviour, and then most of them returned to their original perching sites. Few shift flights subsequently followed within at least 5 min after the encounter. Thus, they perched at the same site and no adults flew away, indicating that there is no territoriality in *M. hirosei* males, and that the face-to-face hovering of females to males may be a mate refusal behaviour. Figure 4 shows that immature adults experienced about 2 encounters per hour in half the number of observed shift flights. Four and five encounters per hour for mature males in the morning and the noon, respectively, suggested peak activity, probably due to reproductive behaviour.

During the observation time, a total of 5 females in 2000 were found to land on the roots or dead reeds which project into the water and commenced oviposition movements. Females oviposited alone. The duration of oviposition lasted less than 1 hour. Diurnal change in the number of females observed is shown in Figure 5, with the number of copulations. Tandem flights were not observed.

Feeding activity was apt to increase in the afternoon for every adult (Fig. 6). They

tried to attack very small insects such as Hymenoptera and Diptera. However, about a half of their attacks on flying insects failed. Instead, they fed on small aphids on the blades or stems of reeds.

DISCUSSION

The present study revealed that the endangered damselfly, *M. hirosei*, is restricted to a small closed habitat where it exhibits few flight activities. The low relative light intensity on the reed community floor was comparable with that of the forest floor (WATANABE et al., 2002), suggesting that the lower level of activity of *M. hirosei* was a result of lower thoracic temperatures under lower ambient temperatures. In fact, some damselfly species inhabiting the forest floor prefer to the sunlit forest gaps (WATANABE et al., 1987). KIRKTON & SCHULTZ (2001) observed that perching damselflies in gaps were able to attain operative body temperatures similar to adults along streams that were open, and pointed out that the additional solar radiation in the gaps may improve the visual acuity of the damselflies searching for prey. However, in the present study, there were no light gaps in the dense reed community floor. The thermal environment due to radiation may also not increase the rate of sexual maturation of *M. hirosei*, and thus they probably exhibit a different behavioural state that cannot be attributed to body temperatures.

ZEISS et al. (1999) reported that *Coenagrion puella* was large prey for a water bug, *Notonecta glauca*. Many kinds of predators such as fishes, frogs, aquatic insects, and so on were recorded for damselfly adults, particularly for females during submerged oviposition (FINCKE, 1986; MICHIELS & DHONDT, 1990; ROWE, 1994). Thus, the low height of the perching site of *M. hirosei* must increase predation risk, because of the presence of frogs and spiders inside the reed community. We observed that *M. hirosei* adults were killed by frogs and *Ischnura senegalensis* along the margins of the reed community, which is open. However, little increase in predation risk may be caused

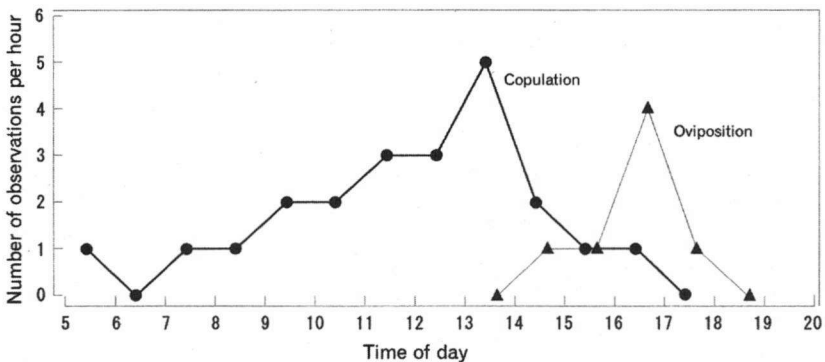


Fig. 5. Diurnal changes in the number of couplings and that of ovipositing females of *M. hirosei*.

by exposure to more predators at the perching sites of *M. hirosei*, under low light intensity among dense reed stems. Birds are unable to enter the dense reed community floor. The discovery and capture of cryptically coloured adults by potential predators also seems less likely. Oviposition alone and no tandem flight might also decrease the adult mortality, because tandem pairs generally present a bigger target of predators than single individuals.

For sexually immature males, the number of shift flights in a day was calculated as 60, based on 4 per hour during a 15-hour day. The number of interrupted flights in a day and the number of encounters were less than 30 and 30, respectively. Therefore, about 120 flight activities were performed for immature males in a day. When 15 feeding flights in a day were added, total flight duration must be less than 3 min per day, since each flight lasted less than 1 sec, strongly indicating that *M. hirosei* is a true percher. Using marked animals, WATANABE & MIMURA (2003) clarified that the immature stage lasted 5 days after emergence, and that mature stages lasted maximum about 30 days. Every shift flight of the immature males was about 15 cm, thus the accumulated length of the shift flights was 9 m in a day, and 45 m during immature stages.

The difference between behavioural activities in immature and mature adults has been noted in many *Zygotera* (e.g. LUTZ, 1968; UEDA, 1978; CORBET, 1980). For sexually mature adults of *M. hirosei*, the number of shift flights in a day was about 90, and the number of interrupted flights and encounters were 40 and 40, respectively.

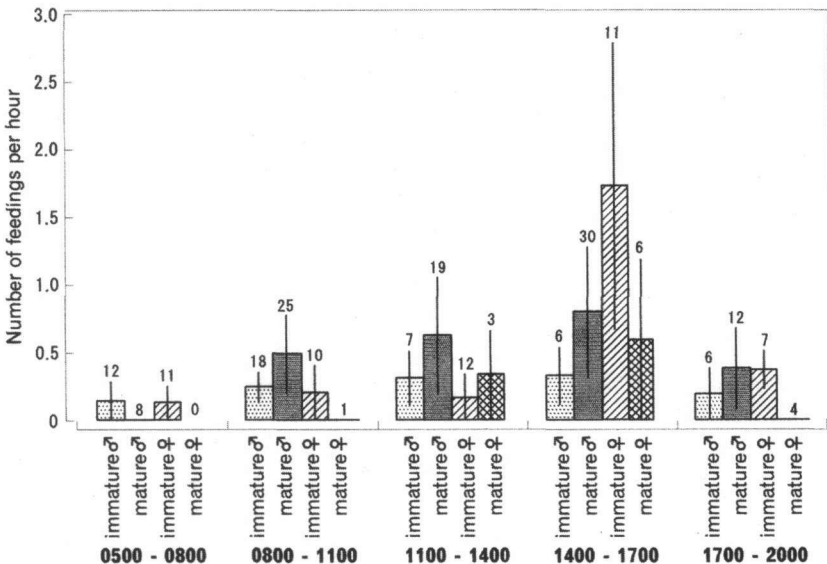


Fig. 6. Diurnal changes in the number of feeding actions of *M. hirosei* at immature and mature stages. Each bar represents SE. The numbers above the symbols show sample size during the three-hour measurement period.

Then, mature adults showed about 170 flight activities with 6 min of total flight duration per day. About 30 cm of each shift flight distance showed that their accumulated length was 27 m per day, for a total of 810 m during the mature stages. Therefore, the accumulated length of shift flights was 855 m during a maximum life span within the reed community. Because this habitat is isolated and 50 m in length and 10 m in width, however, each adult must show about 9 round trips in the reed community, suggesting that many encounters must take place when the population density reaches its peak. Although many encounters between and/or among adults occurred resulting in fighting behaviours, such as face-to-face hovering, no male territorial behaviour was seen in the understory of the reed community as reported by HIROSE & KOSUGE (1973). The high density throughout the flying season suggests that this species does not exhibit territoriality (WATANABE & MIMURA, 2003).

The coexistence of mature and immature individuals as well as of both sexes in the reed community can be expected to affect the flying and reproductive behaviour of every adult, since they changed the diurnal rhythm of their flight activities from immature to mature stages. Mating behaviour and oviposition behaviour were observed in the morning and the afternoon, respectively. Feeding behaviour was increased in the afternoon for both sexes, but the success of predation was not accurately measured though a considerable number of attacks almost failed. In addition, we did not determine the factors that caused shift flight behaviour in *M. hirosei*. During shift flights lasting less than 1 sec, they did not encounter flying conspecifics. On the other hand, an encounter did not lead to a shift flight by every adult.

ASKEW (1982) reported that the mean height above ground level of roosting damselflies *Ischnura elegans*, *Coenagrion puella*, and *Enallagma cyathigerum*, was about 80 cm. In contrast, the height above ground or water level of perching *M. hirosei* was about 20 cm throughout the day, probably including roosting height during the night. The occurrence of males and females together on such a reed community floor raises the possibility of some inhibition of the unwilling mating behaviour of females at certain times. However, this trait in perchers showed a few accidental encounters, and no abnormal couplings, such as mature males with immature females, were observed though they co-existed. Since the time of the peak frequency of shift flights by mature males roughly coincided with the time of the couplings, it is suggested that females have a diurnal physiological rhythm for the acceptance of males.

In non-territorial Zygoptera, the aggregation of solitary males at available oviposition sites has been explained as a mate-finding tactic (e.g. BANKS & THOMPSON, 1985). The operational sex ratio at the oviposition site is biased in many damselfly species, forcing males to interfere with each other (e.g. UEDA, 1987; FINCKE, 1982). However, solitary males do not interrupt oviposition in tandem for *Lestes* species (WATANABE & MATSUNAMI, 1990; STOKS, 2000). In *M. hirosei*, there was a high density of solitary males and females in the reed community floor which is the oviposition site: 2 adults per square metre, with a sex ratio near unity (WATANABE & MIMURA, 2003). They were invariably found to perch low, near the water's surface on the stems

of dense reeds, resulting in a closed and dark perching site, and very poor visibility for damselflies. Tandem pairs and ovipositing females were seldom disturbed by solitary males. In general, because a female insect with a short life span should try to limit the costs of copulation and minimize the time it takes to complete oviposition, she may avoid an unnecessarily high frequency of copulation (MARTENS & REHFELDT, 1989). Therefore, such non-interference by solitary adults including immature and mature males favours the adults aggregating in the community floor where males encounter their mates, though there must be an additional mechanism to prevent releasing unnecessary courtship behaviour.

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