

DIURNAL CHANGES IN MALE MATE PREFERENCE TO FEMALE DIMORPHISM IN *ISCHNURA SENEGALENSIS* (RAMBUR) (ZYGOPTERA: COENAGRIONIDAE)

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I. senegalensis ♀♀ exhibit colour dimorphism as andromorphs and gynomorphs, to which males seem to switch their mate preference according to prior copulation experience. In the field where andromorphs were dominant, the binary choice experiments were conducted both in the early morning, which marks the onset of daily copulation activity, and in the afternoon, which marks the end of the copulation activity. During the former period, ♂♂ showed fair selectivity, while they preferred the andromorphs in the afternoon, suggesting that ♂ mate preference to each ♀ morph switched in relation to copulation experience; i.e. the mating attempts of ♂♂ were biased to the dominant ♀ morph. Mating attempts in the afternoon were considered to inhibit ♀ oviposition behaviour, resulting in a decrease of her reproductive success. Therefore, biased ♂ mate choice toward the dominant morph in the afternoon might be a selective force to maintain the ♀ colour dimorphism.

INTRODUCTION

Studies of female colour dimorphism have been reported in several odonate species (CORDERO & ANDRÉS, 1996), among which female coenagrionid damselflies appear as andromorphs, being quite bright and resembling the conspecific males, and gynomorphs, exhibiting cryptic coloration. FINCKE (2004) suggested that female colour dimorphism has evolved as a response to sexual harassment resulting from the mate-searching behaviour of males. In general, males prefer the dominant female morph in the female population, because forming a search-image of the dominant female morph might be advantageous in terms of reduced the searching time (VAN GOSSUM et al., 2001), resulting in more fre-

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quent mating attempts for the dominant female morph than for the other female morphs (MILLER & FINCKE, 1999). Such male mating attempts might hinder the dominant female morphs from foraging, and consequently reduce their egg development rate and the number of eggs laid (SVENSSON et al., 2005). Therefore, a low frequency of male harassment allows rare female morphs to forage freely and to lay more eggs. Selective male harassment of dominant female morphs consequently equilibrates the fitness of both female morphs; that is, female dimorphism seems to be balanced by a negative frequency-dependent selection (SVENSSON & ABBOTT, 2005).

MILLER & FINCKE (1999) suggested that male mate preference for a particular female morph changed with the frequency of encountering each female morph. Although the effects of sexual interactions on male mate preference have not yet been clarified (e.g. VAN GOSSUM et al., 2001), TAKAHASHI & WATANABE (2008) indicated that male mate preference for female morphs in *Ischnura senegalensis* was switched depending not on males' experience with encountering female morphs but rather on their copulation experience. Male mate preference might change with the diurnal rhythm of mating activity, because *I. senegalensis* males copulated in the morning when females showed sexual receptivity (SAWADA, 1999). However, there have been no reports on changes in male mate preference in relation to mating activity in the field. In the present study, we compared the male mate preference after mating activity with that before mating activity in the field.

MATERIAL AND METHODS

Both males and females of *I. senegalensis* stay in the grassland near water all day long. Males actively search for their mates throughout the day but do not establish any territories along the water-side. Copulation is observed in the early morning and lasts until noon, and then females alone start to oviposit on the leaves or stems of floating plants (e.g. SAWADA, 1995). Males try to mate with the females that are ovipositing in the afternoon, though few females accept the copulation. When ovipositing females encounter mate-searching males, most females escape from the males, or reject the males using a mate refusal display, i.e. hovering face-to-face, fluttering, and bending the abdomen.

Field experiments were conducted in grasslands along a pond located in Omitama-city, Ibaraki, Japan (36°15'N, 140°19'E). To estimate the frequency of each female morph in the local population, we used a line transect method. Four lines (40 m each) were set up in the grassland by the water. Each line was patrolled in the morning (10:00-11:00), during which most females stayed in the grassland. We recorded the sex, female morph and age (mature and immature) of each individual detected within 1 m to either side of the line while walking.

The binary choice experiment was conducted with the wild males perching in the grassland. Both andromorphs and gynomorphs, which were captured in the same local population, were pinned on each end of a Y-shaped stick (ca 1 m) just after being killed by carbon dioxide gas. The female pair was gently put in front of a perching male, in order to release the mating behaviour of the males. A male mating attempt directed at a female morph was judged as an indication of the male's preference. According to the diurnal activity rhythm of *I. senegalensis*, the binary choice experiment was carried out in the early morning (07:00-08:00) and afternoon (13:00-14:00), corresponding to periods before and after copulation activities in the field, respectively.

RESULTS AND DISCUSSION

Solitary males and females that perched on the tips of grass blades with intermittent flying were observed in the survey grassland in the early morning. After that, males began to search for females on the wing in the grassland, dashed to females and then the copulation began. Most of the copulation was continued through the morning, and terminated at around noon.

According to the line transect in the morning, 28 males and 27 females in total were detected along the 4 census lines. Twenty-six out of the 28 males were identified as sexually mature. There were one immature andromorph and 2 immature gynomorphs. Fourteen mature females found were copulating (8 andromorphs and 6 gynomorphs). Ten mature females were perching alone, including 8 andromorphs and 2 gynomorphs. Thus, the andromorph was the dominant morph (66.6%) in the female population, though there have been no reports on andromorph-biased populations in female dimorphic *Ischnura* species. For *I. damula* and *I. demorsa*, the frequencies of andromorphs were less than 27% and less than 42%, respectively (JOHNSON, 1975). For *I. ramburii*, 25 to 31% of females were andromorphs (ROBERTSON, 1985). Therefore, the male mate preference for female dimorphism in the *Ischnura* species has hitherto been investigated in such gynomorph-biased populations, and the males were expected to prefer gynomorphs (e.g. SIROT et al., 2003).

In the binary choice experiment in the field, each male immediately dashed to the pinned females and tried to copulate. In the early morning, males exhibited fair selectivity between female morphs (Tab. I). MILLER & FINCKE (2004) also reported that the male mate preference for female morphs of *Enallagma civile* is fair early in the day, while the males preferred the dominant female morph in the afternoon.

In the afternoon, solitary *I. senegalensis* females visited near the water to start to oviposit. Although males were still searching for females during the afternoon, females did not accept copulation, showing mate-refusal behaviour or escaping from the males. The binary choice experiment in the afternoon indicated that the males significantly chose andromorphs, which were the dominant morph in the female population (Tab. I). *E. boreale* males also preferred andromorphs

Table I
The number of males that chose each female morph in the binary choice experiment both in the early morning and the afternoon

	Andromorphs	Gynomorphs	χ^2	
Early morning	8	10	0.22	n.s.
Afternoon	15	3	8.00	P<0.01

when andromorphs outnumbered gynomorphs (FORBES, 1994), though males were usually apt to prefer gynomorphs over andromorphs, as suggested by ROBERTSON (1985). *I. senegalensis* males in the laboratory preferred the same female morph with which they had mated (Y. TAKAHASHI & M. WATANABE, 2008), suggesting that wild males that had copulated with andromorphs in the morning might be apt to prefer andromorphs in the afternoon. Consequently, male mating attempts in the afternoon might interfere with dominant female that attempts to oviposit, or might directly interrupt oviposition behaviour, probably reducing the reproductive success of dominant female morphs.

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