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Competitive Habitat Utilization in the Damselfly, *Mnais nawai* (Zygoptera: Calopterygidae) Coexisting with a Related Species, *Mnais pruinosa*

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Abstract. Reproductive behaviors related to habitat utilization were studied in males of the damselfly, *Mnais nawai*, which has two male forms, territorial orange-winged males (*nawai*) and non-territorial pale-orange-winged males (*sahoi*), at the upper part of a mountain stream where they partially coexist with a related species, *Mnais pruinosa*, which also has two male forms, territorial orange-winged males (*esakii*) and non-territorial hyaline-winged males (*strigata*). These two species showed parapatric distribution; the lower part of the stream was occupied by *M. nawai*, and the upper part by *M. pruinosa*. In the present study, cross-matings occurred between both *Mnais species*, although normal intraspecific matings occurred more frequently than cross-matings. Territorial males of both species copulated with conspecific females that entered their territory and guarded the ovipositing females, probably to avoid sperm displacement resulting from subsequent copulations. Severe competition for oviposition sites by territorial males even occurred between the two species. On the other hand, non-territorial males of both species have alternative mating strategies (including several tactics such as sneaking, takeover and interception). The possible benefits from conflict among territorial males of both species is discussed.

Key words: *Mnais*; male polymorphism; mating strategy; territory; interspecific competition.

Introduction

At the beginning of the century, mathematical studies on the ecology of species indicated that a species was an assemblage consisting of uniform individuals (Lotka 1925; Volterra 1926). In fact, however, every population of a species includes a variety of individuals having age or phenotypic variation (Lomnicki 1988), even in the case of interspecific interactions occurring between two or more species. It is clear that inter-specific interaction does not work equally for all individuals constituting a population. We found that an intraspecific difference of reproductive behavior in each species played an important role in the interspecific interactions between two partially sympatricly related damselflies, *Mnais nawai* and *M. pruinosa*.

Mnais nawai and *M. pruinosa* were considered to be subspecies of the genus *Mnais* in the early stages of classification (Asahina 1976). However, it was recently suggested that *M. nawai* and *M. pruinosa* actually represent two distinct species (Suzuki 1984; Ishida et al. 1988). The precise systematic relationship of these two *Mnais* species has not been clarified as yet (Hamada and Inoue 1985). In this study, field investigations were performed under the assumption that *M. nawai* and *M. pruinosa* are different species in accordance with Suzuki (1984) and Ishida et al. (1988).

In the damselfly, *M. nawai*, a population of the two male forms *nawai* (orange-winged males) and *sahoi* (pale-orange-winged males), and one female form, *nawai* (pale-orange-winged females), was seen near Fukuoka City, Japan (Nomakuchi 1992). The *nawai* males were territorial and the *sahoi* males were usually non-territorial in nature. Likewise, *M. pruinosa* also had a population of the two male forms, *esakii* (orange-winged males) and *strigata* (hyaline-winged males), and one female form, *sieboldi* (hyaline-winged females) coexisting at the same site. The *esakii* males were territorial and the *strigata* males were usually non-territorial in nature (Nomakuchi

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et al. 1984).

Reproductive behavior of dragonflies has largely been explained with regard to sperm displacement: male sperm in the female storage organ is removed and exchanged with the latter male's sperm through multi-copulation of the female (Waage 1979). In Japanese *Mnais* species, the existence of several reproductive strategies or tactics in a population has been discussed in terms of the sperm displacement phenomenon (Nomakuchi 1988; Nomakuchi and Higashi 1985; Siva-Jothy and Tsubaki 1989a, b; Watanabe and Taguchi 1990). Nomakuchi (1992) argued that *esakii* males are 'guarding strategists' which try to prevent females they copulate with from recopulating with other males by guarding them throughout the oviposition period to avoid sperm displacement, and that *strigata* males are 'multi-copulation strategists' which, rather than holding a territory in the stream, try to copulate as frequently as possible, employing alternative behaviors to catch females as follows: sneaking into *esakii* males' territories to copulate with ovipositing females, intercepting females on branches hanging over the stream (satellites), and waiting for females resting and feeding in the forest area at a distance from the stream. But they can not ensure that their own sperm fertilizes a female's eggs because they do not guard the female after copulation. It is of interest to clarify whether or not the two male forms of *M. nawai* have reproductive strategies similar to those of *M. pruinosa*.

We investigated a population of *M. nawai* from the viewpoint of its relationship with *M. pruinosa*, in a recently found partially sympatric habitat in which *M. nawai* and *M. pruinosa* coexist (Nomakuchi 1992). In the present report, we describe typical characters related to population parameters and reproductive behavior of *M. nawai*, and discuss how interspecific interactions influence intraspecific relations during reproduction.

Study area and methods

The studies were carried out at the upper part of the Muromi River in Fukuoka City, Japan. The study area expanded from the junction of two branch rivers at the upper site to about 100 m downstream, and constituted the precise area where two parapatrically distributed *Mnais* species (*M. nawai* lived downstream; *M. pruinosa* lived upstream) coexisted (Nomakuchi 1992). One side of the stream in the study area was bush and the other side was cultured farmland. There was a large sand dune in the center of the stream. The width of the stream was about 20 m, including the sand dune, and the depth 10–50 cm. The space above the stream was largely open but some trees on the bank of one side hung over the water surface shading a part of the stream neighboring the bank. The open area of the banks and the sand dune were densely covered with reeds which were also distributed in the stream, while some other plants, butterbur and honewort, occurred in the shaded area of the stream. These plants in the water area, as well as algae and dead trees in the stream, were found to be oviposition substrates.

Population censuses were performed 15 times every other day, in principle, from 25 April to 22 June in 1980. Adults were captured with an insect net and each was marked on the left hindwing with fast-drying ink. Marked adults were released after sex, wing and abdominal length, degree of maturation and behavior before being caught were recorded, and the location was noted on a hand-written map of the stream. At subsequent discoveries of these adults, individual number, behavior and location were recorded without actually capturing the insects. Territory sites were numbered and each was marked by a tag or coloration near the perching site of a territorial male. Copulations and ovipositions which were seen during the censuses were also recorded to determine the frequency of these behaviors, and the incidence of cross-mating. The number of adults was estimated by the Manly and Parr (1968) method.

On sunny days, selected territorial males of *M. nawai* form *nawai* were observed several times (for 20 minute intervals per trial) from 12:00 to 15:00 in the reproductive season to clarify the types of aggressive behavior used to repel intruders from their territory. A total of 72 observations were made on 12 different *nawai* males (maximally 26 times per male). Aggressive behaviors were classified into five types based on the severity of the fight, as described by Nomakuchi et al. (1984), after the works of Jacobs (1955), Pajunen (1964, 1966a, b), Ubukata (1979), Arai (1982), Higashi (1981), and Higashi and Uéda (1982). The five patterns were: (A) a male pursues another male unilaterally; (B) two males pursue each other, changing their flight route; (C) two males' flight routes form concentric loops, consisting of a succession of sharp turns within a limited area (circle flight); (D) following a circle flight, two males fly up gradually to a height of ca 1.5 m, hovering parallel with each other and making sudden climbs and return dives of ca. 30 cm (rocking flight); and (E) during the rocking flight, two males quickly fly upward to a height of ca. 10 m (dual flight). We verified which types of aggression patterns were observed during a fight, and counted the frequency of the different types between male forms of both *Mnais* species.

A cross-mating experiment was performed to determine whether or not mating occurred between the two *Mnais* species. Tethered females of *M. nawai* and *M. pruinosa* were put in turn near perching males of each form of both *Mnais* species and the response of the males was observed. If the male approached the tethered female and formed a tandem, the tethered female was pulled from the male and a tethered female of the other species was introduced to the male. Each mating trial was stopped before copulation to avoid the influence ejaculation may have had on the motivation of the male toward the next mating. If the male did not respond to the tethered female within five minutes (failure), that female was replaced with a female of the other species. Five *nawai* males, five *sahoi* males, five *esakii* males and three *strigata* males were selected for this experiment, and one of six pairs of females (*nawai* and *sieboldi* females) was introduced to each male once, in principle. The same female pair was introduced about three times to different males.

Results

Body characters of M. nawai *and* M. pruinosa

Adult males and females of both *M. nawai* and *M. pruinosa* were frequently recognized in the study area. Body characters of damselflies of both species captured in the mark and release census are shown in Table 1. *M. nawai* consisted of orange-winged males (*nawai*), pale-orange-winged males (*sahoi*) and pale-orange-winged females (*nawai*), while *M. pruinosa* consisted of orange-winged males (*esakii*), hyaline-winged males (*strigata*) and hyaline-winged females (*sieboldi*). The abdomen and wing lengths of *M. nawai* were larger and longer than those of *M. pruinosa*. As the characters of both males and females differed markedly between species, it was easy to identify them even in the field. Although *nawai* males were similar to *esakii* males, we could discriminate them in the field by differences in body size and costal opaque streak size.

Reproductive and territorial period of M. nawai

The number of individuals of each type of *M. nawai* were estimated using the data from the mark and release censuses, and the seasonal changes were examined (Fig. 1). The reproductive period of orange-winged males (*M. n.* f. *nawai*) began in late April, and the density of these males reached a peak in early May and gradually decreased, thereafter, until the reproductive season ended in late June. Seasonal changes in density of pale-orange-winged males (*M. n.* f. *sahoi*) and females (*M. n.* f. *nawai*) were fairly similar to those of *nawai* males. Although the shape of the curve for the mean estimated number of *sahoi* males appears to be different from that of *nawai* males and females, an accurate comparison of the patterns is difficult because of the high SD values. The reproductive period of the related species, *M. pruinosa*, occurred during the same season and nearly overlapped that of *M. nawai* (Nomakuchi 1992). The peak in density appeared to be slightly delayed, probably because of juvenile habitat preference: immature *M. pruinosa* have a greater tendency than immature *M. nawai* to stay at a distance from the stream until maturation.

As new adults of *Mnais* damselflies spend about one week after emergence as reproductive immatures, mature adults began to appear in mid-May. Figure 2 shows the seasonal changes in the actual number of mature and/or territorial males of each species discovered in the stream. The number of mature males of *M. p.* f. esakii, *M. n.* f. *nawai* and *M. n.* f. *sahoi* also changed synchronously. *M. p.* f. *strigata* males showed a similar phenological pattern (Nomakuchi 1992). The earliest territorial male was observed in the study area on May 11th in the case of *M. n.* f. *nawai* and on May 14th in the case of *M. p.* f. *esakii*. Thereafter, the actual number of territorial males of *nawai* and *esakii* changed synchronously. Earlier in the season (mid-May to the end of May), non-territorial males were observed in the study area, but they were not seen later (from June 1 to mid-June). Also, the actual number of territorial males fluctuated earlier in the season, but became stable later on. This may indicate that conflicts

Table 1. Characters of *M. nawai* and *M. pruinosa*.

Species	Sex	Form	N	Wing color	Costal opaque streak[a]	Abdomen length[b] (mean ± SD)	Left hind wing length[c] (mean ± SD)
M. nawai	m	*nawai*	96	orange	large	46.0 ± 1.6	39.9 ± 1.4
	m	*sahoi*	80	pale orange	none	44.1 ± 1.4	37.7 ± 1.2
	f	*nawai*	137	pale orange	none	41.3 ± 1.3	39.5 ± 2.0
M. pruinosa	m	*esakii*	29	orange	none or small	43.2 ± 1.8	36.5 ± 1.3
	m	*strigata*	152	hyaline	none	42.0 ± 1.6	35.0 ± 1.5
	f	*sieboldi*	104	hyaline	none	38.4 ± 1.4	36.8 ± 1.2

[a] The costal and subcostal cell-rows were opaquely tinted around the nodus.

[b] Abdomen length was significantly different for pairs in all combinations of form and sex ($0.01 < P < 0.05$ between *M. n.* f. *sahoi* males and *M. p.* f. *esakii* males, and *M. p.* f. *esakii* males and *strigata* males; $P < 0.001$ for the other pairs, *t*-test).

[c] Left hind wing length was significantly different for every pair ($P < 0.001$, *t*-test) except *M. n.* f. *nawai* males and *nawai* females ($0.05 < P < 0.1$, *t*-test), and *M. p.* f. *esakii* males and *sieboldi* females ($0.1 < P < 0.5$, *t*-test).

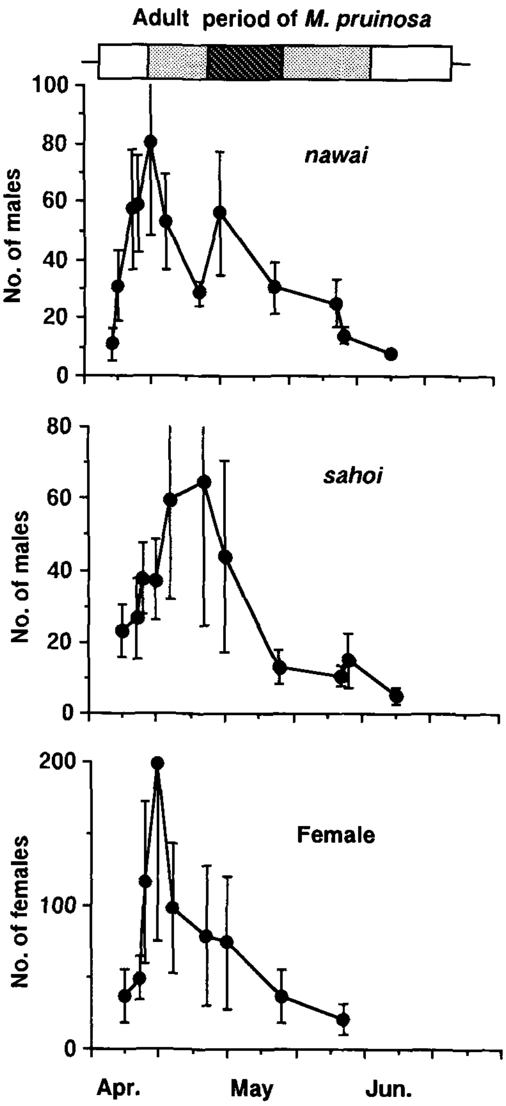

Fig. 1. Seasonal changes in the estimated number of males and females of *Mnais nawai*. The band at the top shows the reproductive period of *M. pruinosa* which was described in Nomakuchi (1992): ☐, low density period; ░, intermediate density period; ▨, high density period.

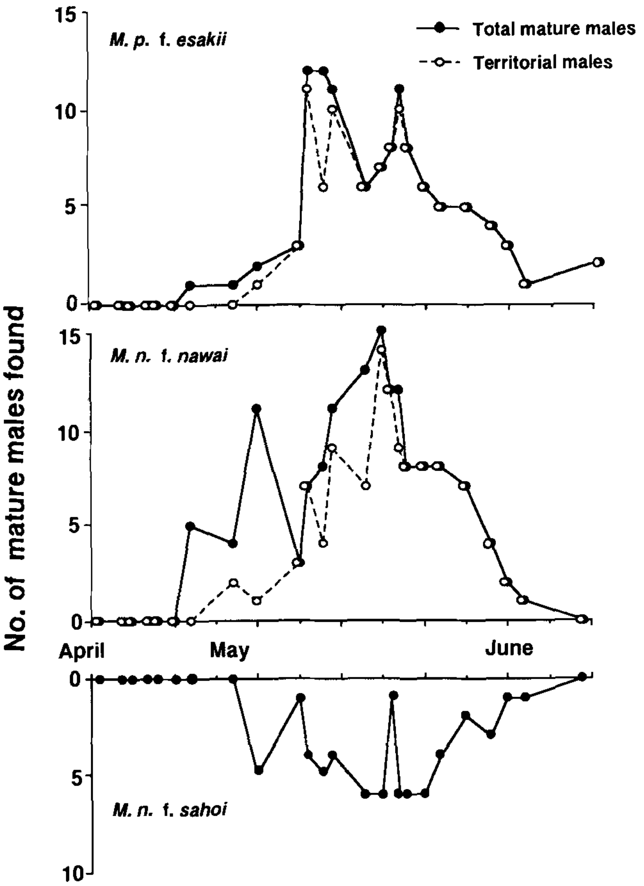

Fig. 2. Seasonal changes in the number of mature and/or territorial males of *Mnais nawai* and *pruinosa* which were discovered during the mark-and-release censuses. Reproductively immature males are excluded from this figure.

for a suitable territory site actually occurred in the earlier period, and the territory of all mature males of *nawai* and *esakii* were stably established in the later period. The average density level of territorial males of *M. n.* f. *nawai* appears to be slightly higher than that of *M. p.* f. *esakii*.

Territorial and non-territorial behavior

Males of *M. n.* f. *nawai* established territories along the edge of the stream, including a perching site and oviposition site in the territory (Fig. 3). Territorial *nawai* males usually perched on rocks, dead trees and plant leaves, etc. at a height of about 10 cm above the water surface, and sometimes patrolled throughout the territory. Perching sites appeared to be fixed in each territory. Territorial *nawai* males aggressively rushed at and fought with intruders when another conspecific male or an *M. pruinosa* male entered the territory. In all cases, the territorial *nawai* males won the fight. When a territorial male encountered a conspecific female in its territory, it approached the female and displayed a simple courtship behavior: the male hovered in front of the female, landed on her wings or dorsal thorax and formed a tandem position unless the female moved away to reject him. The territorial *nawai* male subsequently copulated with the female on a plant leaf or a rock in the territory. The female then oviposited in the territory and the territorial *nawai* male guarded her.

Two or more territorial males never had simultaneous ownership of the same territory, although different males sequentially possessed the same territory because of changes in territory ownership. Territory sites appeared

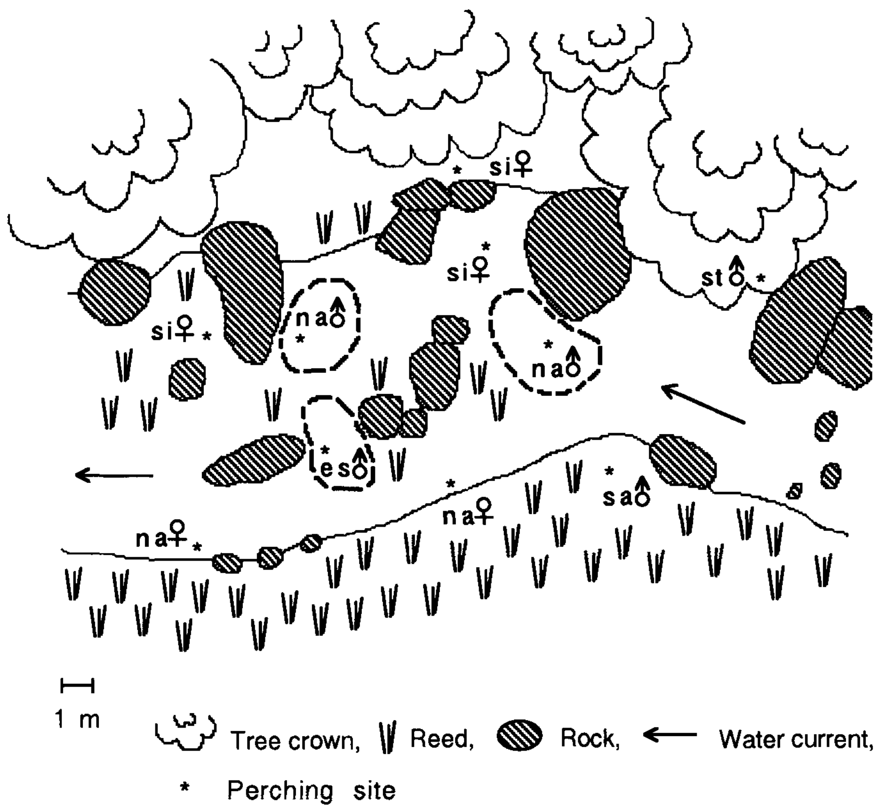

Fig. 3. The location of males and females of *M. nawai* and *M. pruinosa* in the stream. Asterisk indicates perching site of *M. n.* f. *nawai* males (na), *M. p.* f. *esakii* males (es), *M. n.* f. *sahoi* males (sa), *M. p.* f. *strigata* males (st), *M. n.* f. *nawai* females (na) and *M. p.* f. *sieboldi* females (si). Broken line indicates territory areas of *M. n.* f. *nawai* and *M. p.* f. *esakii*.

to be strictly determined by males because they included an oviposition site which rarely shifted even if the territory owner changed. Changes of territory ownership apparently occurred not only between conspecific males but also between interspecific males, because some territories and perching sites were observed being held and used by territorial orange-winged males of each species on different days (Fig. 4). Although none of the following events were directly observed, we suspect these changes in ownership were caused by aggressive interactions between an owner and an intruder, or the disappearance of an owner because of death or movement to a more suitable place. Changes in territorial ownership apparently occurred more frequently in the earlier reproductive period, while non-territorial orange-winged males were still present. However, it decreased in the later reproductive period when non-territorial orange-winged males had become rare. A comparison of the utilization of territory sites by the two species was carried out by Morisita's (1959) R_δ-index. The index of correlation, R_δ, between *M. nawai* (w) and *M. pruinosa* (p) is described as:

$$R_\delta = C_\delta - W_\delta \qquad (R_\delta \geq 0)$$

or

$$R_\delta = (C_\delta - W_\delta)/W_\delta \qquad (R_\delta < 0)$$

where $W_\delta = 2/(\delta_w + \delta_p)\,q$, and q is the number of territory sites (here $q = 46$). δ for each male form and C_δ are defined as:

$$\delta_w = \sum_{i=1}^{q} n_{wi}(n_{wi} - 1)/N_w(N_w - 1),$$

$$\delta_p = \sum_{i=1}^{q} n_{pi}(n_{pi} - 1)/N_p(N_p - 1),$$

and

$$C_\delta = \sum_{i=1}^{q} n_{wi}\, n_{pi}/(\delta_w + \delta_p) N_w\, N_p$$

where, n_{wi} and n_{pi} are the utilization frequency of i-th territory site by each species. N_w and N_p are the total utilization frequencies of each species, respectively. R_δ takes a value of zero if the two species appear independently in each territory site. When no territory site is utilized by the two species, R_δ becomes -1, and when a perfect positive correlation is found between the two species, it becomes $+1$. The calculated value of -0.286 indicates that there was a negative correlation of periods for which a given territory was occupied by territorial males of the two

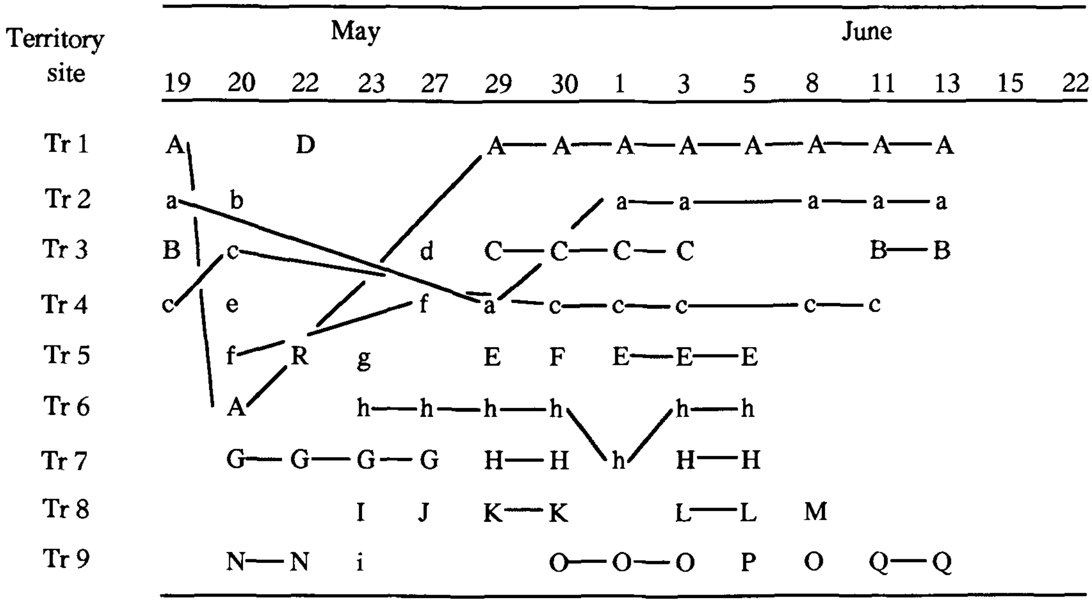

Fig. 4. The pattern of competitive territory occupation and ownership alternation between two territorial *Mnais* males. Nine territory sites, which territorial males frequently utilized, were selected and shown. Different letters in the figure indicate different territorial males which were found to stay exclusively at a territory site on a mark and release census: capital letters indicate *M. nawai* f. *nawai*; lower letters indicate *M. pruinosa* f. *esakii*. Same letters are connected by a solid line where possible.

species: a territory site which males of one species frequently utilize is less likely to be utilized by males of the other species.

Males of *M. n.* f. *sahoi* were usually non-territorial, perching on plant leaves or rocks at a height of about 1 m above the water surface around the territory sites of *M. n.* f. *nawai* or *M. p.* f. *esakii* males (satellite behavior) (Fig. 3), as were the *strigata* males of *M. pruinosa* (Nomakuchi 1992). They sometimes sneakily intruded into a territory of *nawai* or *esakii* males and attempted to take over an ovipositing female, but were unsuccessful in most cases because the territory owner immediately found such intruders and drove them out of the territory. It was also found that *sahoi* males intercepted females about to enter the territory, and intercepted females feeding at bushes along the stream. In the later reproductive period, *sahoi* males were occasionally observed perching in the stream at a height of about 10 cm above the water surface at sites which had been occupied by a territorial *nawai* or *esakii* male; these males sometimes pursued other *sahoi* or *strigata* males. If *nawai* or *esakii* males moved into the area, however, the *sahoi* males soon began to behave like non-territorial males.

Intra and interspecific aggressive behaviors

Aggressive behaviors of territorial males of *M. n.* f. *nawai* were observed in the field to determine the tactics they employ to repel intruders. Territorial males of *M. n.* f. *nawai* responded aggressively to conspecific males and *M. pruinosa* males but not to those of another genus, *Calopteryx*, in the same family which were also seen along the stream.

Territorial males of *M. n.* f. *nawai* frequently showed severe aggressive behavior towards other males of *M. n.* f. *nawai* and *M. p.* f. *esakii* which intruded into their territory (Table 2). But, when an intruder was a male of *M. n.* f. *sahoi* or *M. p.* f. strigata, the territorial *nawai* males only drove them out of the territory: the fight usually did not escalate to more severe patterns of aggression and was apparently a ritual. During these observations of aggressive behaviors of territorial *nawai* males, no change of territorial ownership ever occurred, although territorial *nawai* males fought a total of seven times with *nawai*

Table 2. Frequencies of different patterns of aggressive behavior between males.

Males	Aggressive behavior				
	A	B	C	D	E
na–na	4	3	3	3	1
na–sa	42	6			
na–es	19	9	3	1	
na–st	197	10			

na, *M. n.* f. *nawai*; sa, *M. n.* f. *sahoi*; es, *M. p.* f. *esakii*; st, *M. p.* f. *strigata*. A, pursuing; B, pursuing each other; C, circle flight; D, rock flight; E, dual flight; see text for details.

Table 3. Frequency of female appearance within a 1 m radius of the perching site of territorial males throughout all censuses.

Territorial male	Total territory[a]	Female	
		M. n. f. *nawai*	*M. p.* f. *sieboldi*
M. n. f. *nawai*	106	33	23
M. p. f. *esakii*	96	5	18
Total	202	38	41

[a] Total territory, cumulative number of territories discovered throughout all mark-and-release censuses.

Table 4. Total copulation frequencies observed throughout all mark-and-release censuses.

Female	Male				Total
	nawai	*sahoi*	*esakii*	*strigata*	
M. n. f. *nawai*	3	4	0	1	8
M. p. f. *sieboldi*	2	2	2	14	20

males, 48 times with *sahoi* males, 28 times with *esakii* males and 207 times with *strigata* males.

Fights between *sahoi* and *strigata* males were sometimes seen during the mark and release censuses. Comparatively severe aggressions were observed at that time.

Cross-mating in nature

Females of both *Mnais* species visited an oviposition site for reproductive behaviors (copulation and oviposition) only. They were found to rest and feed at a distance from the oviposition sites. Resting *M. nawai* females were often discovered on leaves of plants in open areas of the sand-bank in the stream, while *M. pruinosa* females were often discovered at shaded areas of the forest along the stream. But females of both species apparently copulated and oviposited in the same areas of the stream. Two oviposition types in females of both species were seen in the field: a single oviposition outside a territory and an oviposition guarded by a territorial male inside a territory. Females of both species usually oviposited on dead trees in open areas of the stream, where *nawai* and *esakii* males had usually established territories. *Nawai* females also oviposited on algal stems which temporarily emerged in the earlier reproductive period but soon disappeared because of increased water current. On the other hand, *sieboldi* females sometimes oviposited, mostly unattended, on emergent stems in shaded areas of the stream.

Table 3 shows the frequency of appearance of both *Mnais* females within a radius of 1 m of the perching site of both territorial *Mnais* males during all censuses. Females were counted regardless of the behavior they displayed (perching only, copulating or ovipositing). Both *Mnais* females clearly visited territories of both nawai and *esakii* males. An independence test between total frequencies of female appearance and total number of male territories observed during all mark-and-release censuses showed that *nawai* females visited territories of conspecific males (*nawai*) more frequently (Fisher's exact probability test, $P=0.00003$), and that *pruinosa* females had no tendency to visit territories of alternative species males (Fisher's exact probability test, $P=0.125$).

Copulations discovered during all mark and release censuses were recorded. In addition to normal intraspecific copulations, a few cross-species copulations were recognized in the field (Table 4). Cross-copulations were observed between *M. nawai* females and *M. pruinosa* males, as well as between *M. pruinosa* females and *M. nawai* males. The ratio at which *M. nawai* females copulated with *M. nawai* males and *M. pruinosa* males was 7/1, and the ratio at which *M. pruinosa* females copulated with *M. nawai* males and *M. pruinosa* males was 4/16, indicating that, in the field, intraspecific copulations occurred more frequently than cross-species copulations (Fisher's exact probability test, $P=0.002$). In a few cases, the process of mating from encountering to the end of copulation could be observed. During these observations, we could discern no behavioral difference between intra- and inter-specific copulations.

Cross-mating field experiment

In order to determine whether or not each species of male responds in a similar manner to females of the same or different species, a cross-mating experiment was perform-

Table 5. Results of the cross-mating experiment. Frequencies of tandem formation and failure (no response or failing in tandem by a male) when tethered females of *M. nawai* and *M. pruinosa* were put in turn near perching males of each form of both *Mnais* species.

Male		*M. nawai* female		*M. pruinosa* female		Tandem/failure	
		Tandem	Failure	Tandem	Failure	*nawai*	*pruinosa*
M. nawai	*nawai*	2	3	1	5	6/4	2/9
	sahoi	4	1	1	4		
M. pruinosa	*esakii*	1	4	2	4	1/7	4/5
	strigata	0	3	2	1		

ed in the field. It was found that each male form of both species tended to form a tandem with females of the same species rather than with those of the other species (Table 5). Upon encountering a conspecific female, the ratio of males that formed a tandem to those that did not was 10/9; on the other hand, the ratio was 3/16 on encountering a female of the other species, indicating that males of both species formed a tandem with conspecific females more frequently than they did with those of the other species (Fisher's exact probability test, $P=0.017$).

Discussion

Coexistence between the two Mnais *species*

The precise systematic relationship between the two *Mnais* species remains unclear. The present findings clearly indicated that *M. nawai* and *M. pruinosa* coexisted in the study area. This fact supports the opinion that *nawai* and *pruinosa* are, indeed, different species, if the premise that subspecies can not coexist is valid.

We also observed cross-matings between the two species in the present study as reported earlier by Suzuki et al. (1980): *M. nawai* males mated with *M. pruinosa* females, and *M. pruinosa* males mated with *M. nawai* females. It is not clear whether or not a hybrid species can emerge in the field; however, at least in this study, no intermediate type between the two species was seen. Therefore, it is unknown whether reproductive isolation works effectively where the two species coexisted. To be sure, from the cross-mating experiment, males had a greater tendency to attempt formation of the tandem position with females of the same species. This shows that they can discriminate between mates of the same and the other species, although errors in recognition of a mate often came about. Thus, ethological isolation may operate between the two species to some extent. It may be that they speciated recently in geological terms, as *M. nawai* resembles *M. pruinosa* not only in wing and body characters but also in the terminal appendix of the abdomen (Hamada and Inoue 1985). Similarly, the fact that competition between the two species of *Mnais* is intense, yet absent between *Mnais* and the sympatric *Calopteryx* species, also suggests that the two *Mnais* species are closely related.

Habitat segregation and reproductive isolation between the two *Mnais* species has been generally recognized (Eguchi 1980; Suzuki et al. 1980). *Mnais nawai* inhabits the relatively lower reaches of a mountain stream, that is characterized by open area with reeds and other emergents (Nomakuchi 1992). *Mnais pruinosa* inhabits the upper reaches of the mountain stream, that is usually covered by the tree crown and, thus, is slightly dark. The two species may be adapted to the environmental characteristics of their respected habitats. However, it might also be possible that they expand their habitat toward the other's habitat in the absence of the other species because both species females can utilize the same oviposition substrate, dead trees. At least in the present study, it was found that disadvantageous conditions (competition for territorial sites and mating error) for both *Mnais* species arose in the partially sympatric area of their parapatric distribution. Nothing is known about competition for resource by nymphs. Therefore, strong factors (e.g. gene flow or environmental change), which can break such disadvantageous conditions, appear to be necessary to operate on the relationship between the two *Mnais* species in this coexisting area for a shift in the present balanced boundary of their distribution.

Mating strategy

Mnais nawai f. *nawai* males showed entirely the same behavior as *M. pruinosa* f. *esakii* males in relation to male-male aggression, mating behaviors and other territorial behaviors; *M. nawai* f. *sahoi* males similarly displayed behaviors identical to those of *M. pruinosa* f. *strigata* males. We described and defined 'multi-copulation strategy' and 'guarding strategy' in *M. pruinosa* as shown by Nomakuchi (1988, 1992), Nomakuchi and Higashi (1985) and Nomakuchi et al. (1984, 1985). *Strigata* males (hyaline winged male, usually non-territorial) showed territorial behaviors when territorial *esakii* males were experimentally excluded from suitable oviposition sites where females frequently visited. However, in fact, *strigata* males could not hold their own territories in the field, because of the presence of *esakii* males. Although *strigata* males can establish their own territories at vacant and unsuitable sites in the stream, they do not do so and choose to stay as non-territorial males around the territory of *esakii* males, where females are likely to make frequent visits. These *strigata* males may copulate more frequently with females, but can not be assured of paternity because the female may recopulate with territorial *esakii* males at the oviposition site. On the other hand, *esakii* males even establish territories at unsuitable sites, if the more suitable sites have already been occupied by other *esakii* males. These *esakii* males can guarantee their paternity by guarding, but rarely encounter females at such poor territories. Therefore, *strigata* males remain at the more suitable sites as non-territorial males apparently because they can encounter females more frequently (multi-copulation strategist), and *esakii* males even establish territories at unsuitable sites to guarantee their paternity by guarding (guarding strategist). Furthermore, the reproductive success of *esakii* and *strigata* males was not dependent on how long they employed their strategy, as their longevities were not different, at least in the adult stage (Nomakuchi et al. 1988). We concluded from the field observations in the present study that *nawai* and *sahoi* males have exactly the same reproductive relationship as that between *esakii* and *strigata* males, although we did not investigate the point as thoroughly as in the previous study of *M. pruinosa.*

Intraspecific effects of interspecific interactions

In the present study, It was found that interspecific influence on a male of the same species differed according to the reproductive strategy, 'guarding strategy' or 'multi-copulation strategy', which was employed by the male. Intense conflict apparently occurred among the 'guarding strategists' (*M. n.* f. *nawai* and *M. p.* f. *esakii*) regardless of their being different species: they showed severe aggressions to compete for territorial areas (oviposition sites). On the other hand, there was only ritual aggression between 'guarding strategists' and 'multi-copulation strategists'. This is probably because they have different goals: 'guarding strategists' ensure fertilization by their own sperm; 'multi-copulation strategists' increase the frequency of copulations. Nomakuchi (1992) already reported that *M. p.* f. *esakii* males suffer a decrease in available territory area, and, thus, a decrease in encounter rate with conspecific females, due to the existence of *M. n.* f. *nawai* males, because *esakii* males can not catch females entering the territory of an *M. n.* f. *nawai* male. *M. p.* f. *strigata* males benefit by sneaking or intercepting conspecific females around a territory of *M. n.* f. *nawai.* Likewise, it seems that *M. n.* f. *nawai* males may be at a disadvantage coexisting with *M. p.* f. *esakii* males; on the other hand, *M. n.* f. *sahoi* males may not.

Although severe aggressions were seen between *M. n.* f. *sahoi* and *M. p.* f. *strigata* when two individuals appeared close to each other, they may not substantially influence each other's reproductive success unless they mistake a mate because they do not remain as territorial males at a specific site. Furthermore, disturbance by males of the other species on the mating between a male and a female of the same species may not be severe because normal matings usually occurred more frequently in the field.

In the present study, character displacement as shown by Suzuki (1984) and Waage (1975) was unclear in both *Mnais* species. It might be that interspecific interaction leads to a change of form ratio of the same species in partially sympatric areas rather than a change of the individual character, as both *Mnais* species already have male polymorphism. In fact, the ratio of *esakii* and *strigata* males was more biased toward *strigata* males in the coexisting area than in the upper part of the stream inhabited solely by *M. pruinosa* (Nomakuchi 1992). Although we have still not made a detailed comparison between male density in the coexisting area and the lower part of the river that is solely inhabited by *M. nawai,* no difference in male form ratio of *M. nawai* was recognized in the preliminary investigation (unpublished). The competition for territory sites between *nawai* and *esakii* males may result in more severe influence on *esakii* males, with the latter being more likely to be excluded from the coexisting area than the *nawai* males. As shown in Table 3, although half or more *M. pruinosa* females appeared at territory sites of *nawai* males during all censuses, *M. nawai* females mostly appeared at territory sites of conspecific males. This may indicate that *nawai* males tend to occupy more suitable territory sites than *esakii* males. Therefore, the result of Morisita's Rd-index may be explained by the possibility that *nawai* males continuously occupied the more suitable territory sites, and, thus, *esakii* males were eventually forced to remain at the less suitable sites.

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