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EGG PRODUCTION IN *SYMPETRUM INFUSCATUM* (SELYS) FEMALES LIVING IN A FOREST-PADDY FIELD COMPLEX (ANISOPTERA: LIBELLULIDAE)

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Although the larval habitats of *S. infuscatum* are paddy fields, all adults leave the paddy fields for forest gaps after emergence, and remain there during their sexually immature stages. In late summer when they have matured, some visit the paddy fields in tandem flight for oviposition. However, many ♀♀ remain perching in the forest gaps, where no mating behaviour is observed. To evaluate the habitat selection of *S. infuscatum* ♀♀ in the forest gaps, fecundity was examined by means of dissection. In the morning, the ♀♀ remaining in the forest gaps loaded fewer mature eggs (ca 100) than did ovipositing ♀♀ in the paddy fields (ca 300). ♀♀ remaining in the forest gaps throughout the day were not willing to visit the paddy fields for oviposition due to the low egg number loaded. This could be because these ♀♀ were developing their eggs, having loaded more sub-mature eggs (ca 60) than ovipositing females in the paddy fields (ca 30). As a result, in the evening, ♀♀ that had developed nearly 500 eggs appeared. In an artificial oviposition experiment, the ♀♀ in the paddy fields released their eggs significantly faster (60 eggs/min) than did those in the forest gaps (16 eggs/min), and released almost all of their eggs, while the ♀♀ in the forest gaps retained a considerable number of eggs in their ovaries. Although ♀♀ loaded 400 ovarioles irrespective of their age, the number of immature eggs per ovariole decreased with age. Consequently, a ♀ might have laid more than 2000 eggs in her life span. ♀♀ must visit the paddy fields cyclically several times in a single month and stay in the forest gaps during the other days.

INTRODUCTION

Paddy fields are the main habitats for the larval stages of *Sympetrum* spp. in Japan. When they emerge, the tenerals of most species generally embark on various kinds of maiden flights, leaving the paddy fields. For example, *S. frequens* embarks on a long maiden flight for the mountains far from the paddy fields (UEDA, 1988), while *S. pedemontanum* takes the shortest maiden flight and almost always remains in the paddy fields (TAGUCHI & WATANABE, 1985). The lengths of the maiden flights of the other *Sympetrum* spp. lie between these two extremes. The adults of most species enter forests close to the paddy fields, where they stay throughout their sexually immature stages, as shown in *S. eroticum* (TAGUCHI & WATANABE, 1987). HIGASHI (1973) reported that the immature adults of *S. frequens* stay in the forests or woods exclusively, feeding during the day.

After sexual maturation, adult *Sympetrum* spp. return to the paddy fields for reproduction. Their reproductive behaviour has been observed mainly in the morning (KINOSHITA & OBI, 1931). Various oviposition substrates, such as open water, mud, small streams, are supplied in the paddy fields and various oviposition behaviour, including flying in oviposition in tandem above the rice plants, has been reported (e.g., MIZUTA, 1978; ISHIKAWA, 1983; TAGUCHI & WATANABE, 1995).

Except for *S. pedemontanum* (TAGUCHI & WATANABE, 1985), *Sympetrum* females visit the paddy fields for only a short time for oviposition (ARAI, 1983; TAGUCHI & WATANABE, 1984), remaining mostly in forests near the fields. WATANABE & TAGUCHI (1988) stated that since both sexes of *Sympetrum* spp. did not show any mating behaviour in forests, forests might serve as feeding areas and roosting sites but not as rendezvous areas. Females that remain in the forests or woods must produce their eggs while feeding. MICHIELS & DHONDT (1989) stated that *S. danae* females might develop clutches of eggs cyclically and visit water repeatedly only once every few days. Thus, in order to clarify the female's reproductive strategy, information on the female's fecundity in the forests or woods is needed.

S. infuscatum enter the forests near the paddy fields after emergence, remain there throughout their sexually immature stages, and after maturation visit the paddy fields for oviposition in tandem flight in the morning (WATANABE et al., 2005). However, many females have been found in gaps in the forest on the same morning, perching on the tips of twigs or grass blades and showing intermittent feeding flights (WATANABE et al., 2004).

In the present study, the fecundity of sexually mature *S. infuscatum* females, both perching in forest gaps and ovipositing in paddy fields, was examined. Changes in the number of eggs present throughout the whole day in females in forest gaps were investigated by means of dissection. Oviposition activity in forest gaps and paddy fields were measured by dipping the abdomen of hand-held insects and allowing them to release their eggs into vials of water. In addition, we counted the number of ovarioles and immature eggs in order to estimate the number of eggs laid by a female during its lifespan.

STUDY AREA AND METHODS

Sampling of sexually mature females was carried out in the Kamishiro region in Shirouma, Nagano prefecture, a cool temperate zone of Japan. A detailed description of the survey area has been provided by WATANABE et al. (2004). A total of 274 individuals were captured in forest gaps and paddy fields during sunny and windless days in late August of 2001, 2002, 2004, and 2005 (total: 16 days). Perching females in the forest gaps were captured from 0600 to 1800, while ovipositing females in tandem flight in the paddy fields were captured from 0900 to 1200, during which period oviposition activity was high.

Immediately after capture, the tips of the abdomens of 161 of the 274 females were repeatedly dipped vertically in water in vials once per second until they stopped releasing eggs in order to allow the individuals to release their eggs. The duration of egg release was measured. Even if the females released no eggs, the dipping procedure was continued for 3 min, after which the insect was considered unwilling to oviposit. After ovipositing was terminated, the number of eggs released in the vial was counted under a binocular microscope. After the artificial oviposition, each female was placed into 50% ethyl alcohol for dissection to examine the number of eggs remaining in the ovaries.

The remaining females (113 individuals) were not artificially forced to oviposit; they were placed into 50% ethyl alcohol immediately after capture. All the females were dissected in order to count the number of mature and sub-mature eggs in their ovaries. The criterion for classifying the degree of egg maturation has been reported by WATANABE & HIGASHI (1993).

In general, the female abdomen contains many ovarioles. Since *S. infuscatum* have panoistic ovaries and their oocytes are not covered with nursing cells, we counted the number of oocytes aligned on the ovarioles toward the tip. Nine females which were in the early stages of maturation judging by their body colour and wing condition, and 10 females which were in the latest stages were captured and dissected in late August and mid September, respectively. The number of ovarioles in each female was counted directly. The number of oocytes which were not oval but oblong were considered immature eggs based on a random sample of 20 ovarioles. The total number of immature eggs was then calculated.

RESULTS

In the early morning (0600-0900) most females rested, perching in the forest gaps, where no mating behaviour was observed. As shown in Figure 1, They had a load of 160.9±18.3 (S.E.) mature eggs, with a range from 0 to 448.

From 0900-1200, females remaining in the forest gaps had a load of 106.7±13.6 (S.E.) mature eggs, which was significantly lower than the load of those captured in early morning (ANOVA Dunnett t-test, $P = 0.036$). In the paddy fields, we captured females in various oviposition stages during the same period, that is, females that had just started oviposition, those currently laying eggs, and those who had terminated oviposition. Consequently, the number of mature eggs remaining in the abdomen varied, ranging from 0 to 614. However, the mean number of mature eggs carried was 327.4±26.2 (S.E.), which was significantly higher than that of the females remaining in the forest gaps during the same period (Mann--Whitney U-test; $Z = -5.962$, $P<0.001$).

From 1200-1500, the number of mature eggs loaded in the females in the forest gaps was 106.9±11.7 (S.E.), i.e. significantly lower than that found from 0600-0900 (ANOVA Dunnett t-test, $P = 0.042$). In the evening, the females that visited the paddy fields for oviposition returned to the forest gaps, and they had few mature eggs remaining. They mingled with the local female population that had remained in the forest gaps throughout the day. Since the females that remained in the forest gaps must develop their eggs and have accumulated mature eggs throughout the day, there was a large variance in the number of mature eggs loaded by females captured from 1500-1800 (0 to 505 mature eggs). The mean number of mature eggs (110.4±21.3, S.E.) was not significantly different from that found from 0600-

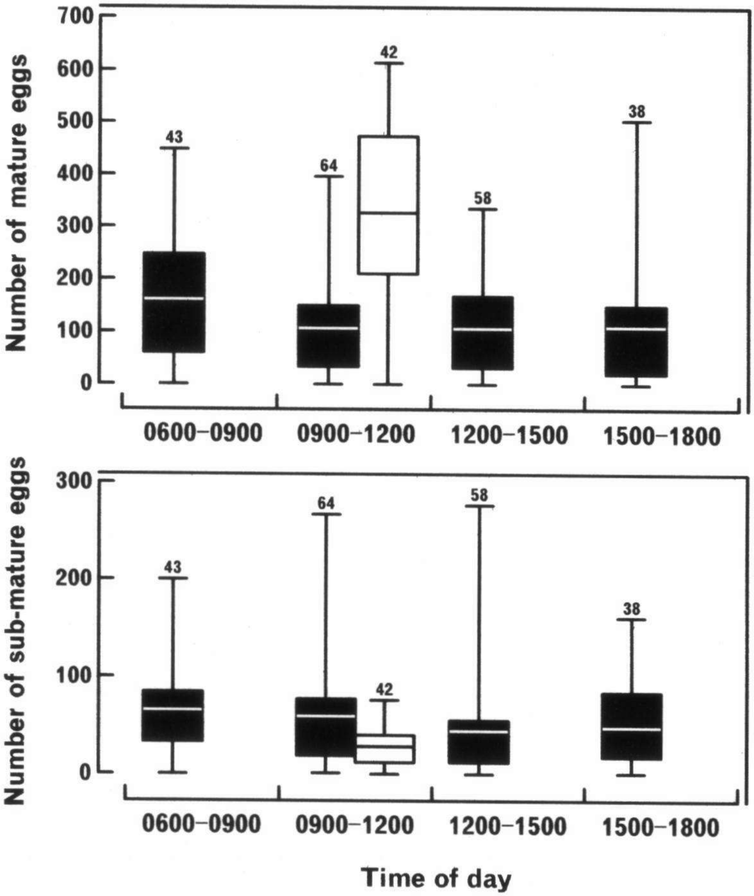

Fig. 1. Diurnal changes in the number of mature and sub-mature eggs of *S. infuscatum* females captured in forest gaps (closed) and in paddy fields (open). The box with the center line represents inter-quartiles with mean value. Bars indicate the range of the smallest and the largest number of eggs in a load. The numeral above each symbol shows the sample size during the three-hour period. The number of mature and sub-mature eggs in the paddy fields were significantly different from those in the forest gaps with a probability of less than 0.001 (Mann-Whitney U-test; Z = -5.962 and Z = -3.676, respectively).

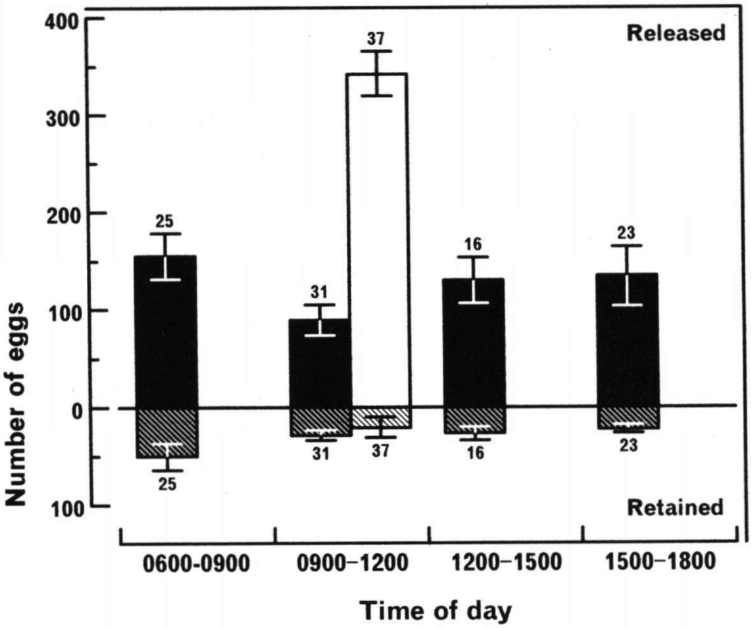

Fig. 2. Diurnal changes in the number of eggs artificially released in forest gaps (closed) and in paddy fields (open) with the number of mature eggs retained in the abdomen. The height of each box represents the mean number. Each bar represents the SE. The numeral above the symbol shows the sample size during each three-hour period. The numbers of eggs released and those retained by the females in the paddy fields differed significantly from those of the females in the forest gaps with a probability of less than 0.001 (Mann-Whitney U-test; Z = -5.991 and Z = -4.617, respectively).

-0900 (ANOVA Dunnett t-test, P = 0.103).

Although the number of sub-mature eggs varied from 0 to 290 throughout the day, most females carried a load of less than 100 sub-mature eggs (Fig. 1). The mean numbers of sub-mature eggs loaded by females remaining in the forest gaps were around 50 to 60 throughout the day, showing no significant difference throughout these periods (ANOVA Dunnett t-test, P = 0.181). On the other hand, females ovipositing in the paddy fields loaded significantly fewer sub-mature eggs, 28.0±3.2 (S.E.), than those in the forest gaps from 0900-1200 (59.3±6.6, S.E.)(Mann-Whitney U-test, Z = -3.676, $P<0.001$).

In the artificial oviposition experiment, every egg released in the vials was normal in size and mature, judging from egg development thereafter. As shown in Figure 2, in the early morning (0600-0900), females in the forest gaps released 154.8±23.1 (S.E.) eggs and retained 50.3±13.9 (S.E.) mature eggs which constituted about 24.5% of all mature eggs they had loaded before the artificial oviposition experiment. From 0900-1200, females released fewer eggs (89.2±15.8, S.E.) and retained fewer eggs (28.6±5.1, S.E.) than that during 0600-0900, although neither value differed (ANOVA Dunnett t-test, P = 0.088 and ANOVA Dunnett t-test, P = 0.144, respectively). Between 1200-1500 and between 1500-1800, the number of eggs released by females in the forest gaps was 129.2±23.2 (S.E.) and 133.7±30.6 (S.E.), respectively. The number of eggs retained were 26.9±6.4 (S.E.) and 22.5±4.2 (S.E.), respectively. Consequently, throughout the day, the number of eggs released and retained by females in the forest gaps did not vary significantly (ANOVA, F = 1.657, P = 0.182 and ANOVA, F = 2.125, P = 0.102, respectively).

Ovipositing females captured in the paddy fields released 341.6±23.3 (S.E.) eggs which was significantly higher than those released by the females in the forest gaps (Mann-Whitney U-test, Z = -5.991, P<0.001). Out of 37 females captured, 22 individuals had no mature eggs in their ovaries after releasing eggs, indicating that they had released all of their eggs. Consequently the mean number of eggs retained was only 20.8±10.6 (S.E.), which was 5.7% of all mature eggs loaded, which was significantly fewer than that of the females in the forest gaps (Mann-Whitney U-test, Z = -4.617, P<0.001).

In the early morning, females in the forest gaps released their eggs within about 6 minutes, with an egg release rate of ca 25 eggs/min (Tab. I). In the subsequent periods, the duration of egg release in the forest gaps decreased to below 5 minutes but showed no significant difference (ANOVA F = 1.629, P = 0.188). The egg release rates were around 24 eggs/min except for the period of 0900-1200 when it was only 16 eggs/min.

The duration of egg release in the paddy fields (5.5 min) did not differ significantly from that in the forest gaps, but significantly higher egg release rates were seen in the paddy fields than in the forest gaps. Although the egg release rate varied widely from 11.3 to 122.0 eggs/min in the paddy fields (Fig. 3), most females exhibited egg release rates of 35-65 eggs/min. Frequency distribution of egg release rates in the paddy fields differed significantly from that in the forest gaps during 0900-1200.

The egg release rates correlated significantly with the number of mature eggs

Table I

Duration of releasing eggs and egg release rates in *Sympetrum infuscatum* in forest gaps and paddy fields

Time of day	Duration of releasing (min, ±S.E.)		Egg release rates (eggs/min, ±S.E.)	
	Forest gaps	Paddy fields	Forest gaps	Paddy fields
0600-0900	6.0±0.5 (25)	-	25.3±3.2 (25)	-
0900-1200	5.1±0.5[a] (31)	5.5±3.4[a] (66)	16.0±2.3[b] (31)	60.0±3.0[b] (66)
1200-1500	4.8±0.6 (16)	-	24.3±3.6 (16)	-
1500-1800	4.5±0.6 (23)	-	23.6±4.2 (23)	-

( ): number of females; – a: Z = -0.32, P = 0.747, Mann-Whitney U-test; – b: Z = -7.18, P<0.001, Mann-Whitney U-test.

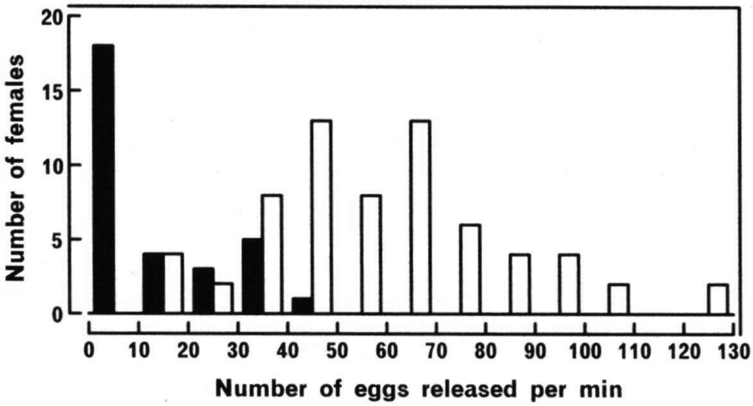

Fig. 3. Frequency distribution of the number of eggs released per minute for *S. infuscatum* in forest gaps (closed) and in paddy fields (open) during 0900-1200. A significant difference occurs between forest gaps and paddy fields with a probability of less than 0.001 (Kolmogorov-Smirnov test; Z = 1.569, P = 0.015).

loaded by females in both the forest gaps and paddy fields (Fig. 4). In the forest gaps, no significant difference was seen between each period (ANCOVA F = 0.065, P = 0.978). In the paddy fields, the intercept of the regression line on the y-axis was higher than that of the females remaining in the forest gaps (ANCOVA F = 12.400, P = 0.001).

Both young and old females captured in the wild had about 400 ovarioles (Table 2). The number of immature eggs per ovariole in the young females was about 22 and thus the fecundity was more than 8800 (= 400×22), while that of the older females was 6800 (= 400×17), suggesting that *S. infuscatum* oviposit more than 2000 eggs over the period between late August and mid September.

DISCUSSION

In Japan, adult *Sympetrum* spp. fly over a wide range, including paddy fields and hills covered with woods or forests, which represent a nursing area, until sexual maturation (WATANABE & TAGUCHI, 1988). After maturation, both males and females return to the paddy fields for reproduction, where territorial behaviour (UEDA, 1979; NARAOKA, 2001), mating behaviour (TAGUCHI & WATANABE, 1985), and ovipositing behaviour (TAGUCHI & WATANABE, 1995; ISHIZAWA, 1998) have been described. They have been observed to be active in the morning for such reproduction in paddy fields (KINOSHITA & OBI, 1931; UEDA, 1979; ARAI, 1983), including *S. infuscatum*, which fly above paddy fields in tandem and oviposit. However, a considerable number of sexually mature females remain in the forest gaps throughout the day, exclusively showing feeding behaviour (WATANABE et al., 2004).

In the present study, *S. infuscatum* females that remained in the forest gaps throughout the day were not willing to visit the paddy fields for oviposition and showed lower oviposition activity than did females in the paddy fields, probably due to the low number of mature eggs loaded. In the early morning, the number of mature eggs loaded was somewhat higher than those in other periods, because some females visited the paddy fields on that day. Consequently, most females in the forest gaps loaded a small number of mature eggs (less than 100) and might not visit the paddy fields during that day. On the other hand, ovipositing females in the paddy fields often had a load consisting of a large number of mature eggs (over 400, sometimes nearly 600). The number of mature eggs in a single clutch has been reported for some *Sympetrum* spp., for example, 241 eggs for *S. flaveolum*, 991 eggs for *S. danae*, and 632 eggs for *S. depressiusculum* (SAHLEN & SUHLING, 2002).

In the artificial oviposition experiment, females captured in paddy fields showed high oviposition activity and released almost their full load of eggs. CORBET (1999) stated that, during each visit to the oviposition site, a female probably lays

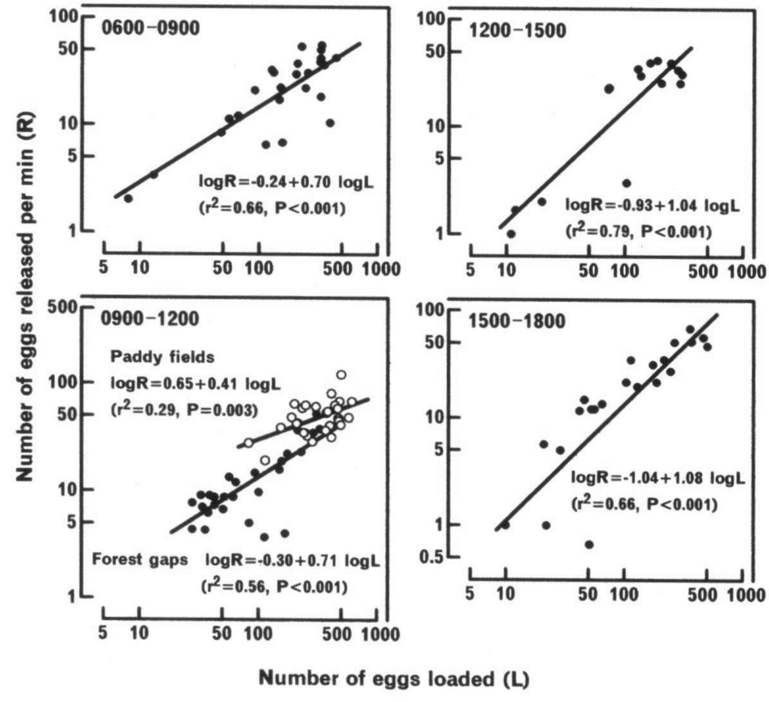

Fig. 4. Correlation between the number of eggs released per minute and the number of mature eggs loaded by *S. infuscatum* females in forest gaps (closed) and in paddy fields (open). Individuals in forest gaps were perching and showing intermittent feeding flights, while in the paddy fields they were ovipositing.

most of the mature eggs in her ovaries if uninterrupted. *S. infuscatum* females in the paddy fields also retained few eggs even after the artificial oviposition, suggesting that they laid their clutch completely and exhausted their mature eggs in the ovaries. A similar oviposition habit was seen in *S. danae* (MICHIELS, 1992). Consequently, females having returned to the forest gaps after oviposition must start developing their eggs. Indeed, in the evening, the mean number of mature eggs loaded by females in the forest gaps was low. HIGASHI & WATANABE (1993) showed that, in *Orthetrum albistyrum speciosum*, the decrease in the number of mature eggs loaded by females in the forests in the afternoon might be a consequence of females returning from the paddy fields after oviposition.

S. infuscatum ovipositing in the paddy fields showed significantly higher egg release rates than did the females in the forest gaps though their duration of oviposition was not significantly longer. This high egg release rate might be caused partly by relatively high abdomen temperatures induced by the radiation temperature in the paddy fields, as shown by McVEY (1984). In late August, since the ambient and radiation temperatures in the paddy fields were higher than those in the forest gaps (WATANABE et al., 2005), the increase in abdomen temperature caused by the radiation temperature in the paddy fields might be a factor leading to the relatively high egg release rates.

The high egg release rate was also influenced by the high number of eggs loaded. Indeed, a positive relationship was seen between the egg release rates and the numbers of mature eggs loaded. This implied that the number of mature eggs loaded was one of the determining factors initiating oviposition activity. WATANABE & HIGASHI (1993) also revealed that the egg release rate increased with the number of mature eggs loaded in *Orthetrum japonicum*.

S. infuscatum might produce several hundred eggs as a clutch laid in one oviposition bout in the manner of other *Sympetrum* spp. (SAHLEN & SUHLING, 2002). Females remaining in the forest gaps might have been developing their eggs during daytime. In the morning, the females in the forest gaps loaded fewer mature eggs and more sub-mature eggs in their ovaries than did the ovipositing females in the paddy fields, suggesting that they were now developing and accumulating their eggs. In the evening, 500 mature eggs appeared in the females that remained in the forest gaps, where they showed a sit-and-wait foraging tactic for

Table II

The number of ovarioles and immature eggs per ovariole (±S.E.) in young females in late-August (n = 9) and old females in mid-September (n = 10)

	Young females	Old females	Mann-Whitney U-test
No. of ovarioles	391.9±11.8 (9)	402.7±17.3 (10)	Z = -0.817, P = 0.414
No. of immature eggs	21.9±0.76 (9)	17.3±0.43 (10)	Z = -3.511, P<0.001

( ): number of females

preying throughout the day (WATANABE et al., 2005). Therefore, a forest gap would provide a feeding area for *S. infuscatum* females for their next bout of oviposition.

MICHIELS & DHONDT (1991) suggested that a certain number of days are needed for eggs to develop in the female ovaries. CORBET (1999) stated that the number of eggs released depended upon the time that had elapsed since the last resting period. *S. danae* females have a 3-4 day inter-clutch interval and, consequently, 66% to 75% of the females were not receptive for mating on a given day (MICHIELS & DHONDT, 1989). WATANABE et al. (2004) reported that in the present survey area more than half of the mature *S. infuscatum* females remained in forest gaps each day. Accordingly, they may remain in the forest gaps for more than two days and repeatedly visit the rice paddies for oviposition.

Odonate females have panoistic ovaries (ANDO & KOBAYASHI, 1996) and a continuous egg production system during their life span. The numbers of ovarioles and immature eggs in an ovariole of some libellulid species have been counted. MIZUTA (1985) reported that an *Orthetrum albistyrum speciosum* female has about 600 ovarioles in each ovary and that each ovariole contains a dozen immature eggs. MATSUZAKI (1971) reported that the number of ovarioles in each ovary of *S. frequens* of unknown ages varied from 250 to 300. In the present study, the number of ovarioles in *S. infuscatum* was about 400 irrespective of their age. The number of immature eggs in an ovariole decreased with age, though JOHNSON (1973) reported that the number of follicles in an ovariole of *Argia moesta* increased with age from teneral to early mature stages. We found that after sexual maturation, assuming that no immature eggs were added and that the number of immature eggs in the ovarioles decreased due to oviposition, more than 2000 eggs were laid from late August to mid September (ca 1 month), though *S. infuscatum* females have the potential to lay roughly 8800 eggs in their lifetime. Since they lay several hundred eggs in each oviposition bout, they must visit the paddy fields cyclically several times in a month and stay in the forest gaps during the remaining days.

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