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Host plant use for oviposition by *Trigonotylus caelestialium* (Hemiptera: Miridae) and *Stenotus rubrovittatus* (Hemiptera: Miridae)

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Abstract The main hosts and sites of oviposition for the two bugs, *Trigonotylus caelestialium* (Kirkaldy) (Hemiptera: Miridae) and *Stenotus rubrovittatus* (Matsumura) (Hemiptera: Miridae), that cause pecky rice were investigated in 24 poaceous plants. Nymphs of *T. caelestialium* emerged from both spikelets and leaf sheaths, while nymphs of *S. rubrovittatus* emerged almost exclusively from spikelets. Suitable plants for oviposition by *T. caelestialium* are *Lolium multiflorum*, *Digitaria violascens* and *Hordeum murinum*, while *Poa annua*, *Anthoxanthum odoratum*, *Alopecurus aequalis* and *D. violascens* were preferentially used by *S. rubrovittatus*. There was a greater difference in the number of nymphs emerging from different plants for *S. rubrovittatus* than for *T. caelestialium*. This difference may be because *T. caelestialium* can oviposit on leaf sheaths if the spikelets are not suitable for oviposition, whereas *S. rubrovittatus* only oviposits on spikelets. Although both bugs oviposited on spikelets, the internal oviposition sites were different. In *D. ciliaris*, *T. caelestialium* laid all eggs between the lemma of the first floret and the second floret, whereas *S. rubrovittatus* laid eggs almost exclusively inside the second floret. In contrast, in *P. annua*, *T. caelestialium* laid all eggs inside the florets, whereas *S. rubrovittatus* laid eggs both between and inside the florets.

Keywords Rice leaf bug · Sorghum plant bug · Poaceous plants · Oviposition preference · Pecky rice

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Introduction

Pecky rice, which is caused by heteropteran bugs, is a major problem that affects rice farming in Japan. The rice leaf bug, *Trigonotylus caelestialium* (Kirkaldy) (Hemiptera: Miridae), and the sorghum plant bug, *Stenotus rubrovittatus* (Matsumura) (Hemiptera: Miridae), have recently received particular attention as major species that cause pecky rice (Watanabe and Higuchi 2006). Brown rice grains may also serve as hosts to both bugs; however, development is poor on the leaves of rice plants (Ishimoto 2008). Therefore, rice is not a major host for these bugs. Hence, rice grains are thought to be damaged by rice bugs that emerge and grow on other poaceous plants adjacent to paddy fields. Because the existence of host plants around paddy fields may affect the abundance of pecky rice bugs, it is important to identify the host plant species. Poaceous plants have been previously reported as a food source for rice bugs, with the removal of grass weeds leading to reduction in rice bug populations (Kikuchi and Kobayashi 2001; Niiyama and Itoyama 2006; Ono et al. 2007; Yokota and Suzuki 2008). However, there have been few reports on the suitability of poaceous plants as hosts for rice bugs.

Trigonotylus caelestialium deposit their eggs into the tight space between the stem and the leaf sheath, whereas *S. rubrovittatus* oviposit into the spikelet (Hayashi 1986;

Kato and Hasegawa 1950; Okuyama and Inoue 1975). In one study, when several grass plants were collected from the field, nymphs of *T. caelestialium* emerged from foliage and spikes, whereas nymphs of *S. rubrovittatus* emerged from the spikes only. This observation further indicated that *T. caelestialium* deposits eggs within the leaf sheath and spikelet, whereas *S. rubrovittatus* deposits eggs into the spikelet only (Nagasawa 2007). Nymphal or larval mobility is generally inferior to adult mobility. Thus, host use by nymphs or larvae is considered to be greatly affected by adult oviposition preferences (Bernays and Chapman 1994; Schoonhoven et al. 2005; Wennström et al. 2010). Therefore, it is important to study the selection of site oviposition to understand host use by phytophagous insects. Several studies have investigated the number of eggs or emerging nymphs on plants collected from fields (Higuchi et al. 2001; Iimura 1992; Nagasawa 2007). However, plant sampling from fields does not show the exact performance of the plants, because the sampling time or site may influence the occurrence of bugs. Oviposition tests have been conducted in some studies (Hayashi 1986; Iimura 1992; Kikuchi and Kobayashi 2004). However, only a few species were studied, and the testing conditions were not comparable. In this study, we investigated oviposition by two rice bug species on various poaceous plants to estimate their potential as host plants.

Materials and methods

Insects

Trigonotylus caelestialium and *S. rubrovittatus* were collected from the experimental field at Hokuriku Research Center, National Agricultural Research Center, Niigata Prefecture, Japan. The insects were reared on young wheat seedlings under laboratory conditions (16L:8D photoperiod, 25 °C), as described previously (Higuchi and Takahashi 2000; Nagasawa and Higuchi 2008, 2010). Adult females of *T. caelestialium* and *S. rubrovittatus* were used for oviposition tests 4–7 and 7–12 days after eclosion, respectively. The preoviposition period of *T. caelestialium* is 3.1 days at 27 °C and 4.4 days at 23 °C (Takahashi and Higuchi 2001). Females of *T. caelestialium* start to attract males within 24 h after eclosion (Higuchi and Takahashi 2002). Therefore, *T. caelestialium* should have mated by the 4th day after eclosion. Mating tests indicated that females of *S. rubrovittatus* started mating with males at 26 h after eclosion and that all females had mated 5 days after eclosion in mating tests (Okutani-Akamatsu et al. 2009). Therefore, almost all females used in this study were considered to have been mated.

Plants

The following 24 poaceous plant species were used in this study (in the order of time of spikes emergence from spring to autumn): *Poa annua* L., *Alopecurus aequalis* Sobol. var. *amurensis* (Komar.) Ohwi, *Anthoxanthum odoratum* L., *Poa sphondylodes* Trin., *Hordeum murinum* L., *Dactylis glomerata* L., *Festuca arundinacea* Schreb., *Vulpia myuros* (L.) C. C. Gmel., *Agrostis clavata* Trin. subsp. *matsumurae* (Hack. ex Honda) T. Tateoka, *Lolium multiflorum* Lam., *Elymus tsukushiensis* Honda var. *transiens* (Hack.) Osada, *Agrostis gigantea* Roth, *Digitaria ciliaris* (Retz.) Koel., *Eragrostis multicaulis* Steud., *Setaria faberi* Herrm., *Echinochloa crus-galli* (L.) Beauv., *Eleusine indica* (L.) Gaertn., *Echinochloa crus-galli* (L.) Beauv. var. *aristata* S. F. Gray, *Oryza sativa* L., *Panicum dichotomiflorum* Michx., *Setaria glauca* (L.) Beauv., *Eragrostis ferruginea* (Thunb.) Beauv., *Digitaria violascens* Link and *Pennisetum alopecuroides* (L.) Spreng (Table 1). All plants, except for the rice *O. sativa* (cultivated in the paddy fields at Hokuriku Research Center), were found growing wild in or around the experimental fields. Because eggs could be laid on these plants by wild females, the collected plants were placed in conical flasks for 2 days at 25 °C before the oviposition tests to distinguish between nymphs derived from eggs laid by test females and those from eggs laid by wild females.

No-choice oviposition test

Twenty-four poaceous plants were collected from the field when the flowering spikes appeared. Sections of stem with 6–7 leaf sheaths and 2–3 spikes were placed in glass sample tubes (10 ml) filled with water. The plant and sample tube were then placed into a cylindrical plastic container (8 cm in diameter × 30 cm in height) with two mesh-covered openings (8 cm in diameter) at the top and around the side. Five adult females were released into the plastic container and then removed after 48 h. Twelve replications of oviposition tests were conducted for each plant at 25 °C, under 16L:8D light conditions. After removing the females, the plants were divided into the stem and the spikes. These plant parts were placed on moist filter paper in a plastic petri dish at 25 °C. At 25 °C, nymphs of *T. caelestialium* and *S. rubrovittatus* are known to emerge at 7–9 and 8–10 days after oviposition, respectively (Nagasawa 2007). Therefore, nymphs that emerged from the plants within 5 days (*T. caelestialium*) and 6 days (*S. rubrovittatus*) after the test were considered to be derived from the wild population and were not counted. *Trigonotylus caelestialium* and *S. rubrovittatus* nymphs that emerged from the plant parts at 6–9 and 7–10 days, respectively, were counted.

Table 1 Poaceae plants used in the oviposition tests

Plants	Subfamily	Tribe	Ear heading period
Poa annua	Pooideae	Poeae	Oct–July
Alopecurus aequalis	Pooideae	Aveneae	Mar–July
Anthoxanthum odoratum	Pooideae	Aveneae	Apr–June
Poa sphondylodes	Pooideae	Poeae	Apr–June
Hordeum murinum	Pooideae	Triticeae	Apr–June
Dactylis glomerata	Pooideae	Poeae	May–June
Festuca arundinacea	Pooideae	Poeae	May–June
Vulpia myuros	Pooideae	Poeae	May–July
Agrostis clavata subsp. *matsumurae*	Pooideae	Aveneae	May–July
Lolium multiflorum	Pooideae	Poeae	May–July
Elymus tsukushiensis var. *transiens*	Pooideae	Triticeae	May–July
Agrostis gigantea	Pooideae	Aveneae	May–July
Digitaria ciliaris	Panicoideae	Paniceae	June–Nov
Eragrostis multicaulis	Chloridoideae	Eragrostideae	June–Nov
Setaria faberi	Panicoideae	Paniceae	June–Nov
Echinochloa crus-galli	Panicoideae	Paniceae	June–Nov
Eleusine indica	Chloridoideae	Eragrostideae	July–Nov
Echinochloa crus-galli var. *aristata*	Panicoideae	Paniceae	July–Nov
Oryza sativa	Bambusoideae	Oryzeae	July–Sept
Panicum dichotomiflorum	Panicoideae	Paniceae	Sept–Nov
Setaria glauca	Panicoideae	Paniceae	Sept–Nov
Eragrostis ferruginea	Chloridoideae	Eragrostideae	Sept–Nov
Digitaria violascens	Panicoideae	Paniceae	Sept–Nov
Pennisetum alopecuroides	Panicoideae	Paniceae	Sept–Nov

Multiple-choice oviposition tests

Ten plant species, which grow in the experimental field at Hokuriku Research Center, were used for multiple-choice oviposition tests. Since the growing seasons of the plants differed among species, the tests were conducted during three different seasons (i.e., spring, summer and autumn). *Poa annua*, *A. aequalis* and *V. myuros* were tested in spring (May–June); *D. ciliaris*, *E. indica*, *S. faberi* and *E. crus-galli* were tested in summer (August–September); and *D. ciliaris*, *E. indica*, *E. crus-galli* var. *aristata*, *P. dichotomiflorum* and *S. glauca* were tested in autumn (October). These plants were placed in sample tubes filled with water, which were then placed in a plastic rearing cage (34 × 25 × 34 cm). Ten adult females were released into the rearing cage and then removed after 24 h. Sixteen replications of oviposition tests were conducted for each seasonal test at 25 °C, under 16L:8D light conditions. Test plants were divided into the stem and the spike. These plant parts were placed on moist filter paper in a plastic petri dish at 25 °C. *Trigonotylus caelestialium* and *S. rubrovittatus* nymphs that emerged 7–9 and 8–10 days after the test, respectively, were counted.

Ovipositional site preference in spikelets

To identify where the insects deposited their eggs in the spikelets of poaceous plants, 8–10 spikelets from *D. ciliaris* and 4–5 spikelets from *P. annua* were placed on moist filter paper in a petri dish (5.5 cm in diameter, 1.5 cm in height). An adult female was released into the petri dish and allowed to oviposit for 6 h. After removing the female, the spikelets were dissected to identify the location of the eggs. Ten females were used for each plant in this test. The structure of the spikelet in *D. ciliaris* and *P. annua* is shown in Fig. 1.
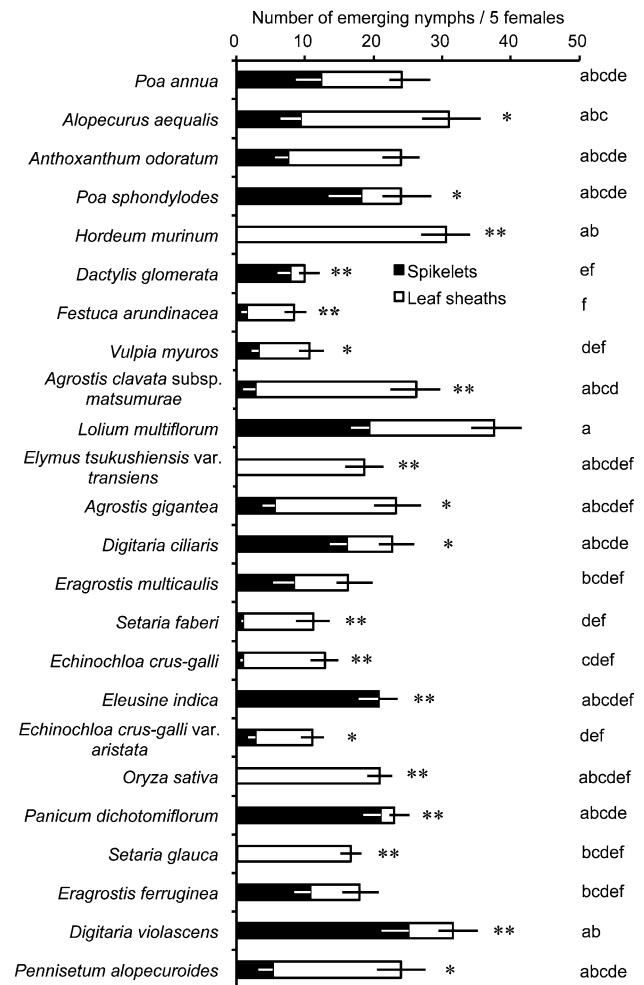
Results

No-choice oviposition test

Relatively large numbers of *T. caelestialium* nymphs emerged from *L. multiflorum*, *D. violascens* and *H. murinum*. Relatively small numbers of *T. caelestialium* nymphs emerged from *F. arundinacea* and *D. glomerata*. However, no significant differences were observed among most plants (Tukey's HSD test after root square transformation,

Digitaria ciliaris
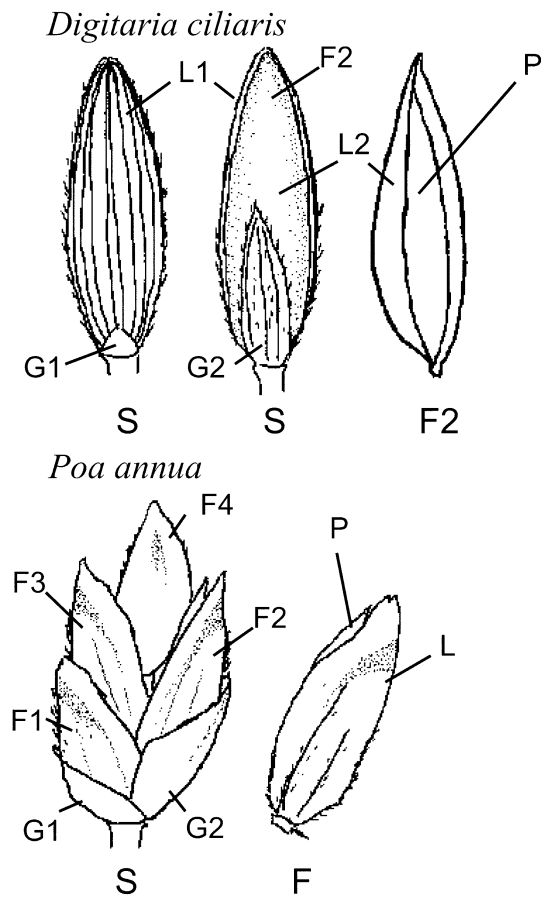
Poa annua

Fig. 1 Spikelets of *Digitaria ciliaris* and *Poa annua*. *S* spikelet, *F1*–*F4* 1st floret–4th floret, *G1*–*G2* 1st glume–2nd glume, *L1*–*L2* lemma of 1st floret–lemma of 2nd floret, *P* palea. There are anthers and a pistil inside each floret. The first floret of *D. ciliaris* is sterile

Fig. 2 No-choice oviposition tests for *Trigonotylus caelestialium*. Adult females were allowed to oviposit on each of 24 poaceous plants for 48 h (12 replications for each plant). Oviposition preference was evaluated from the number of emerging nymphs (not from the number of eggs). *Black bars with white vertical lines* indicate the mean and standard error of the number of nymphs emerging from spikelets (mean − SE). *White bars with lower vertical lines* indicate the mean and standard error of the number of nymphs emerging from leaf sheaths (mean − SE). *Upper vertical lines on bars* indicate the standard error of the mean number of nymphs emerging from whole plants. Significant differences in the means for spikelets and leaf sheaths are indicated as *$P < 0.05$, **$P < 0.01$ (Wilcoxon's signed rank test). Means of emerging nymphs from whole plants with the *same alphabetical letters* are not significantly different (Tukey's HSD test after root square transformation, $P > 0.05$)

$P > 0.05$; Fig. 2). Relatively large numbers of *S. rubrovittatus* nymphs emerged from *P. annua*, *A. odoratum* L., *A. aequalis* and *D. violascens* (Fig. 3). In particular, more *S. rubrovittatus* nymphs emerged from *P. annua* than from the other plants, except *A. aequalis*, *A. odoratum* and *D. violascens* (Tukey's HSD test after root square transformation, $P < 0.05$). In contrast, relatively small numbers of *S. rubrovittatus* nymphs emerged from *O. sativa*, *S. faberi* and *S. glauca* (Fig. 3). In particular, fewer *S. rubrovittatus* nymphs emerged from *O. sativa* than from the other plants, except *S. faberi* and *S. glauca* (Tukey's HSD test after root square transformation, $P < 0.05$). Nymphs of *T. caelestialium* emerged from eggs deposited in both the spikelets and the leaf sheaths, whereas *S. rubrovittatus* nymphs emerged almost exclusively from eggs deposited in the spikelets (Figs. 2, 3). Only a small number of *S. rubrovittatus* nymphs emerged from the leaf sheaths of *P. annua*, *A. aequalis*, *H. murinum*, *V. myuros*, *D. ciliaris*, *E. multicaulis* and *P. alopecuroides*. The relative proportions of *T. caelestialium* nymphs emerging from spikelets and leaf sheaths varied among plant species. The nymphs emerged

from just the leaf sheaths of *H. murinum*, *E. tsukushiensis* var. *transiens*, *O. sativa* and *S. glauca*; however, nymphs emerged from just the spikelets of *E. indica*. More nymphs emerged from the leaf sheaths than from the spikelets of *A. aequalis*, *F. arundinacea*, *V. myuros*, *A. clavata* subsp. *matsumurae*, *A. gigantea*, *S. faberi*, *E. crus-galli*, *E. crus-galli* var. *aristata* and *P. alopecuroides*; however, more nymphs emerged from the spikelets than from the leaf sheaths of *P. sphondylodes*, *D. ciliaris*, *P. dichotomiflorum*
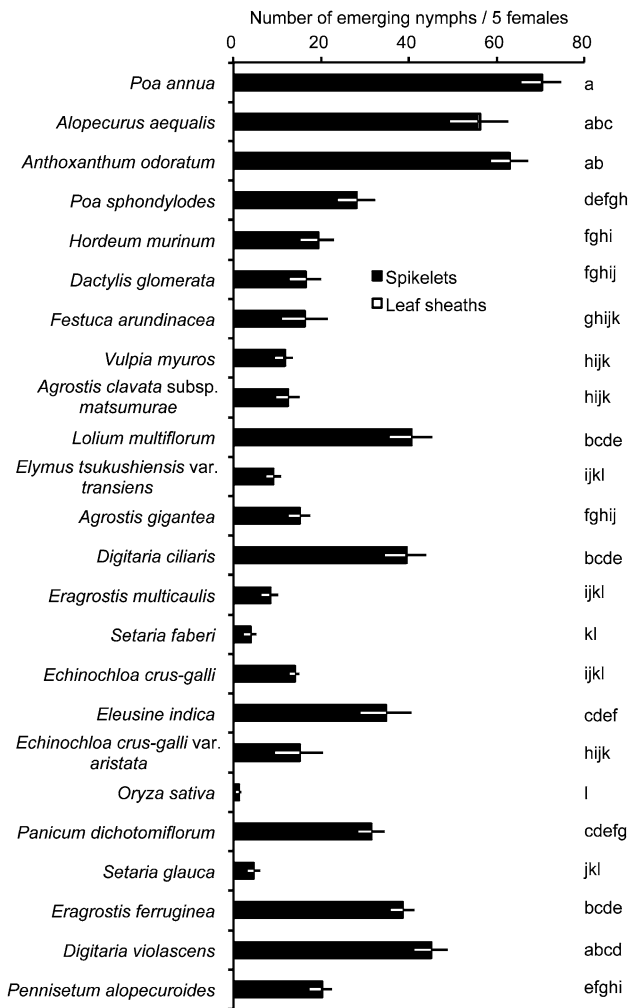
Fig. 3 No-choice oviposition tests for *Stenotus rubrovittatus*. Adult females were allowed to oviposit on each of 24 poaceous plants for 48 h (12 replications for each plant). Oviposition preference was evaluated from the number of emerging nymphs (not from the number of eggs). *Black bars with white vertical lines* indicate the mean and standard error of the number of nymphs emerging from spikelets (mean−SE). *White bars with lower vertical lines* indicate the mean and standard error of the number of nymphs emerging from leaf sheaths (mean − SE). *Upper vertical lines on bars* indicate the standard error of the mean number of nymphs emerging from whole plants. Means of emerging nymphs from whole plants with *same alphabetical letters* are not significantly different (Tukey's HSD test after root square transformation, *P* > 0.05)

and *S. faberi* (Wilcoxon's signed rank test, *P* < 0.05). The number of emerging nymphs was not significantly different between the spikelets and leaf sheaths of *P. annua*, *A. odoratum*, *L. multiflorum*, *E. multicaulis* and *E. ferruginea* (Wilcoxon's signed rank test, *P* > 0.05).
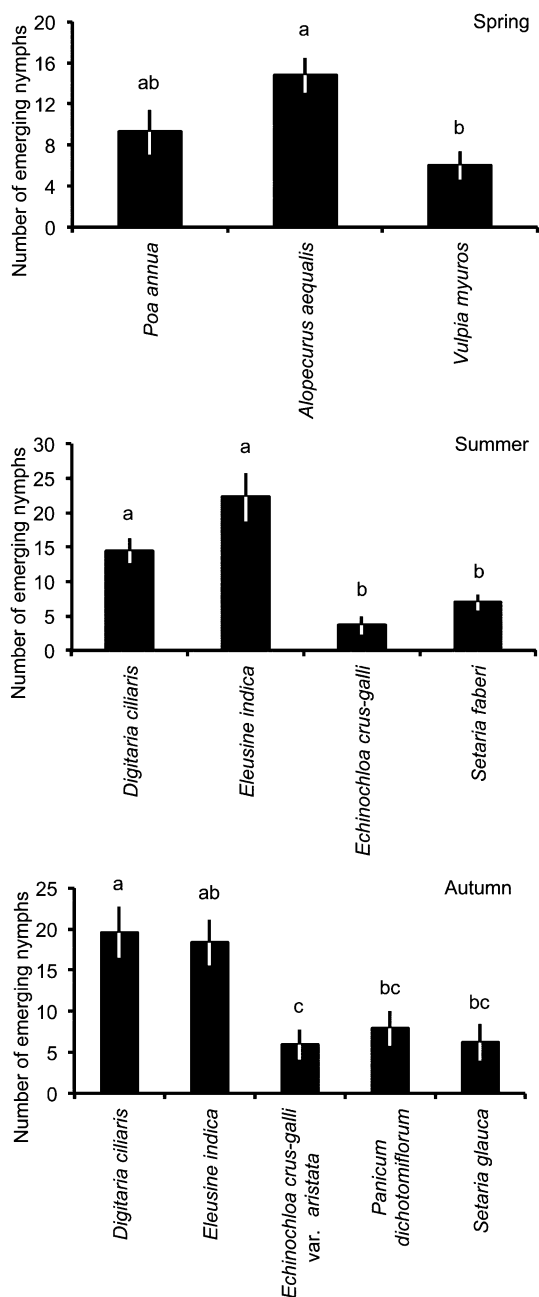
Multiple-choice oviposition test

Among the spring plants, more *T. caelestialium* nymphs emerged from *P. annua* than *A. aequalis* (Wilcoxon signed
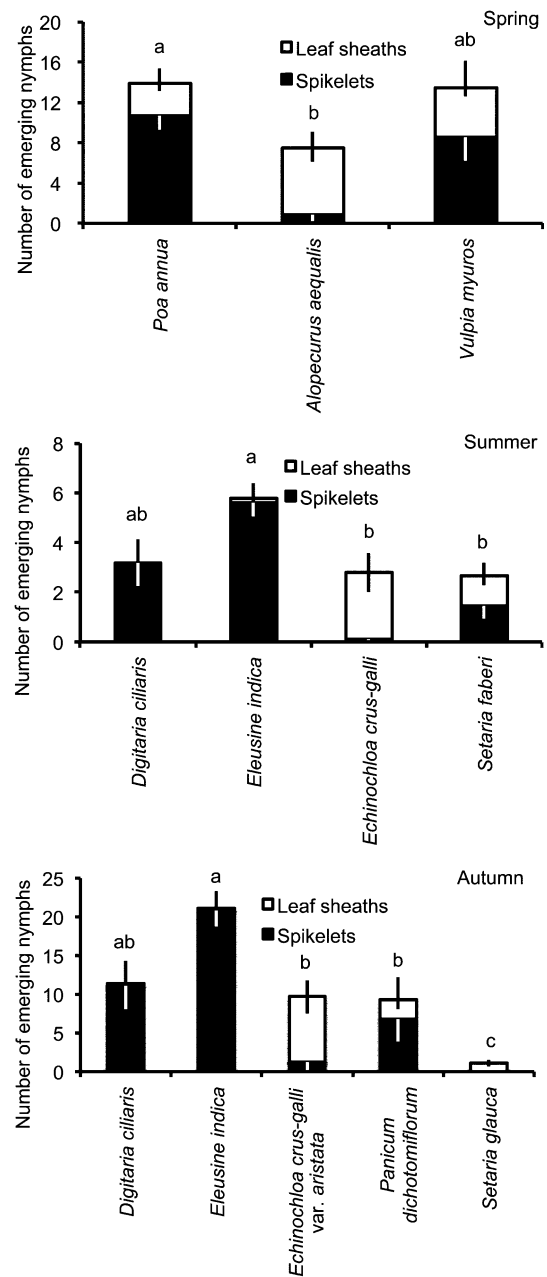
Fig. 4 Multiple-choice oviposition preference tests for *Trigonotylus caelestialium*. Ten adult females were allowed to oviposit on different poaceous plants for 24 h (16 replications for each test). The tests were conducted during three different seasons, i.e., spring (May–June), summer (August–September) and autumn (October). *Black bars with white vertical lines* indicate the mean and standard error of the number of nymphs emerging from spikelets (mean−SE). *White bars with lower vertical lines* indicate the mean and standard error of the number of nymphs emerging from leaf sheaths (mean−SE). *Upper vertical lines on bars* indicate the standard error of the number of nymphs emerging from whole plants. Means followed by the *same letter* are not significantly different (Wilcoxon signed rank test with Holm's correction for multiple comparisons, *P* > 0.05)

rank test with Holm's correction for multiple comparisons, *P* < 0.05; Fig. 4). In contrast, more nymphs of *S. rubro-vittatus* emerged from *A. aequalis* than from *Vulpia myuros*

Fig. 5 Multiple-choice oviposition preference tests for *Stenotus rubrovittatus*. Ten adult females were allowed to oviposit on different poaceous plants for 24 h (16 replications for each test). The tests were conducted during three different seasons, i.e., spring (May–June), summer (August–September) and autumn (October). *Black bars with white vertical lines* indicate the mean and standard error of the number of nymphs emerging from spikelets (mean−SE). *White bars with lower vertical lines* indicate the mean and standard error of the number of nymphs emerging from leaf sheaths (mean−SE). *Upper vertical lines on bars* indicate the standard error of the mean number of nymphs emerging from whole plants. Means followed by the *same letter* are not significantly different (Wilcoxon signed rank test with Holm's correction for multiple comparisons, $P > 0.05$)

(Wilcoxon signed rank test with Holm's correction for multiple comparisons, $P < 0.05$; Fig. 5). Among the summer plants, the most nymphs of *T. caelestialium* emerged from *E. indica,* followed by *D. ciliaris*. Fewer nymphs of *T. caelestialium* emerged from *E. crus-galli* and *S. faberi* than from the other plants (Wilcoxon signed rank test with Holm's correction for multiple comparisons, $P < 0.05$; Fig. 4). More nymphs of *S. rubrovittatus* emerged from *E. indica* and *D. ciliaris* than from *S. faberi* and *E. crus-galli* (Wilcoxon signed rank test with Holm's correction for multiple comparisons, $P < 0.05$; Fig. 5). Among the autumn plants, the largest number of *T. caelestialium* nymphs emerged from *E. indica* followed by *D. ciliaris*, *E. crus-galli* var. *aristata* and *P. dichotomiflorum*. The lowest number of *T. caelestialium* nymphs emerged from *S. glauca* (Wilcoxon signed rank test with Holm's correction for multiple comparisons, $P < 0.05$; Fig. 4). More nymphs of *S. rubrovittatus* emerged from *D. ciliaris* than from *E. crus-galli* var. *aristata*, *P. dichotomiflorum* and *S. glauca* (Wilcoxon signed rank test with Holm's correction for multiple comparisons, $P < 0.05$; Fig. 5).

Ovipositional site preference in spikelets

Trigonotylus caelestialium deposited all eggs between the lemma of the first floret and the second floret of *D. ciliaris*. *Stenotus rubrovittatus* deposited most eggs inside the second floret (between the lemma and the palea) of *D. ciliaris*. In contrast, *T. caelestialium* deposited all eggs inside the florets of *P. annua*. Although *S. rubrovittatus* deposited more eggs inside the florets of *P. annua*, individuals also deposited some eggs between the florets (Table 2). Egg location was significantly different between *T. caelestialium* and *S. rubrovittatus* on both *D. ciliaris* and *P. annua* (Fisher's exact test, $P < 0.001$).

Discussion

It has been previously reported that *T. caelestialium* deposits eggs into the tight space between the stem and the leaf sheath of poaceous plants, whereas *S. rubrovittatus* oviposits into the spikelet (Hayashi 1986; Kato and Hasegawa 1950; Okuyama and Inoue 1975). Moreover, the emergence of nymphs from poaceous plants collected in the field indicated that *T. caelestialium* oviposits into both the leaf sheath and the spikelet, whereas *S. rubrovittatus* oviposits in only the spikelet (Nagasawa 2007). In this study, the rice bugs were given the opportunity to oviposit on 24 poaceous plant species. Almost all *S. rubrovittatus*

Table 2 Total number of *Trigonotylus caelestialium* and *Stenotus rubrovittatus* eggs in the spikelets of two poaceous plants

| | *Digitaria ciliaris* | | *Poa annua* | | |
| | Between L1 and F2[a] | Inside of F2[a] | Between G and F | F | |
				Between[a]	Inside[a]
T. caelestialium[b]	21	0	0	0	30
S. rubrovittatus[b]	4	25	0	13	29

L lemma, *F* floret, *G* glume, *L1* lemma of first floret, *F2* second floret

[a] The proportion of eggs deposited inside florets was significantly different between *T. caelestialium* and *S. rubrovittatus* on both *D. ciliaris* and *P. annua* (Fisher's exact test, $P < 0.001$)

[b] 10 females

nymphs emerged from the spikelets of all the plants. This observation indicates that *S. rubrovittatus* oviposits in spikelets only. However, *T. caelestialium* emerged from both the foliage and spikes of most plants. This observation indicates that *T. caelestialium* oviposits into both the leaf sheath and the spikelet. This study confirmed that this species definitely oviposits in the leaf sheaths because oviposition was directly observed. However, since eggs were not directly observed inside the spikelets (as this requires considerable effort), one reason for nymphs not emerging from some spikelets is that some eggs did not hatch. However, since the emergence of nymphs from the spikelets was observed in some plants, both *T. caelestialium* and *S. rubrovittatus* are clearly able to oviposit in the spikelets. In addition, our investigation using *P. annua* and *D. ciliaris* showed that both rice bugs are able to oviposit in the tight space inside the spikelet. Mirid bugs, like *Macrolophus caliginosus* and *Lygus rugulipennis*, oviposit by drilling into the spaces of plant tissues (Ferran et al. 1996; Romani et al. 2005). In contrast, *T. caelestialium* and *S. rubrovittatus* oviposit into the natural narrow spaces of plant tissues, such as the leaf sheaths or spikelets. Thus, the presence of a suitable space for oviposition is considered as a factor that affects oviposition site selection in both rice bug species. Although both *T. caelestialium* and *S. rubrovittatus* oviposited in the spikelet, the exact sites of oviposition slightly differed. For instance, *T. caelestialium* deposited eggs between the lemma of first floret (sterile) and the palea side of the second floret (fertile) of *D. ciliaris*, whereas *S. rubrovittatus* deposited eggs inside the second floret (between the lemma and the palea). Furthermore, *T. caelestialium* deposited all eggs inside the florets of *P. annua*, whereas *S. rubrovittatus* deposited eggs between adjacent florets and inside florets. These differences may indicate that oviposition cues are different for *T. caelestialium* and *S. rubrovittatus*. It is not clear whether this difference is attributable to the structure of the spikelet or chemical components. However, these factors might contribute to the difference in selection of leaf sheaths for oviposition between *T. caelestialium* and *S. rubrovittatus*.

In the no-choice tests, many *T. caelestialium* nymphs emerged from *A. aequalis*, *A. odoratum*, *L. multiflorum* and *D. violascens*. These plants are suitable for oviposition by *T. caelestialium*. In contrast, only a few *T. caelestialium* nymphs emerged from *D. glomerata* and *F. arundinacea*. These plants may be unsuitable for oviposition by *T. caelestialium*. However, only a small difference in the number of *T. caelestialium* nymphs that emerged from different plants was observed. In comparison, many *S. rubrovittatus* nymphs emerged from *P. annua*, *A. aequalis*, *A. odoratum* and *D. violascens*. These plants are therefore suitable for oviposition by *S. rubrovittatus*. In contrast, only a few *S. rubrovittatus* nymphs emerged from *O. sativa*, *S. faberi* and *S. glauca*. These plants may be unsuitable for oviposition by *S. rubrovittatus*. Compared to *T. caelestialium*, a greater difference in the number of *S. rubrovittatus* nymphs that emerged from different plants was observed. For *O. sativa*, *S. faberi* and *S. glauca*, it should be noted that *T. caelestialium* deposited a few eggs into the spikelets; however, many eggs were deposited into the leaf sheaths. Since *T. caelestialium* oviposits into both the leaf sheath and the spikelet, this species might preferentially select the leaf sheath when the spikelets are not suitable for oviposition. In comparison, since *S. rubrovittatus* only oviposits into the spikelets, the number of eggs deposited on a given plant might decrease because of the absence of an alternative oviposition site when spikelets are not suitable for oviposition. Differences in the choice range of sites between *T. caelestialium*, which can oviposit on both spikelets and leaf sheaths, and *S. rubrovittatus*, which only oviposits on spikelets, may lead to differences in suitable plant ranges for oviposition.

Because the no-choice oviposition tests were only conducted for 48 h, the number of emerging nymphs was probably affected by both the oviposition site selection and egg production derived from plant nutrition. In addition to these factors, we cannot exclude the possibility that the number of emerging nymphs was affected by other factors, such as differences in hatching rates. Therefore, our results may not exclusively reflect the oviposition preference of

these bugs. However, the results of this study are important toward evaluating the potential of each plant as hosts for bugs that cause pecky rice. The plants from which more nymphs emerged should be recognized as the sources of these bugs. These results support previous studies that identified *P. annua*, *D. ciliaris* and *L. multiflorum* as major sources of these two bugs (Hachiya 1999; Hayashi 1986; Kakizaki 2004). While the two mirid bugs laid many eggs on Italian ryegrass, *L. multiflorum*, they laid only a few eggs on orchard grass, *D. glomerata*, and tall fescue, *F. arundinacea*. Therefore, differences in the characteristics of pasture grasses may contain important information for controlling the occurrence of these mirid bugs.

In this study, the multiple-choice tests were conducted for 24 h. However, it is unclear how nutrient intake affects the length of egg production by the two rice bug species. It is likely that the fecundity of individual bugs is at the same level during the 24-h test because a decrease in the number of deposited eggs only occurred after 24 h in a continuous oviposition test in which plants were examined every 24 h (Nagasawa, unpublished data). Moreover, there was no drastic difference in egg numbers in the sampling survey. Therefore, the results of the multiple-choice tests provide a reliable indication of the oviposition preferences of these bugs. *Trigonotylus caelestialium* preferred *P. annua* in spring and *E. indica* in summer and autumn. *Stenotus rubrovittatus* preferred *A. aequalis* in spring and *D. ciliaris* and *E. indica* in summer and autumn. These mirid bugs showed different oviposition preferences among Poaceae plants. However, the factor that influences the oviposition preference of these bugs remains unclear; hence, it is important to investigate the correlation between oviposition preference and nymphal growth, to study host selection of phytophagous insects and to identify the host plants on which these mirid bugs develop.

The existence of grass spikes is essential for the survival of *S. rubrovittatus* and for improving the potential for *T. caelestialium* nymphal growth (Nagasawa and Higuchi, unpublished data). Thus, few nymphs of *S. rubrovittatus* occur in paddy fields, especially before the heading time, because of their low oviposition preference for rice, in addition to the poor growth of nymphs of this species on rice. Moreover, oviposition preference for rice remains low after the heading time. These results indicate that generally *S. rubrovittatus* should rarely occur in paddy fields. However, if grass weeds, such as a barnyard grass, grow in a paddy field, these weeds may act as hosts for *S. rubrovittatus*. Emerging nymphs of *S. rubrovittatus* from the paddy weeds would damage rice in a similar way to *T. caelestialium* nymphs, which are considered to be a major cause of pecky rice (Ishimoto 2004; Ishimoto and Nagase 2005). In contrast, larger populations of *T. caelestialium* are likely to be found in paddy fields because *T. caelestialium* is able to oviposit sufficiently into the leaf sheaths of rice. Plants that have suitable oviposition sites, namely spikelets and leaf sheaths, are important for the occurrence of both rice bug species. Therefore, the closer these plants grow to paddy fields, the more attention they should receive by agricultural management practices, since it is predicted that the rice bugs that emerge from these plants directly cause pecky rice.

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