ORIGINAL RESEARCH PAPER

Spatio-temporal distribution of adults and eggs of the West Indian sweetpotato weevil *Euscepes postfasciatus* (Coleoptera: Curculionidae) on sweet potato stems

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Abstract

The West Indian sweetpotato weevil, *Euscepes postfasciatus*, a serious pest of sweet potatoes, is being eradicated by sterile insect technique (SIT) in the south-western islands of Japan. Information on the diurnal movement of the target pests on host plants and where mating and egg-laying behavior occurs on the host is important for the application of SIT, which eradicates the target pest through mating of released sterile males and wild females. However, little such information is available on this species. In this study, male and female adults were released on host plants to examine the diurnal distribution on seedlings according to sex, as well as the sites where mounting behavior and egg laying occurs. The results showed that females left the host plant more frequently at night, whereas males were more likely to remain on the host plant at night. Both males and females stayed on the nodes of the host plant during the daytime. Mounting behavior also tended to occur more often at nodes. Furthermore, compared to unmated females, mated females stayed at the vertical top of the seedlings. However, it was found that eggs were often laid close to the roots rather than at the top of the vertical stems, even when the seedlings were placed upside down. The results of previous studies and this study will be discussed from the perspective of the application of SIT against *E. postfasciatus*.

Keywords Diurnal pattern · Eggs · Mating system · Mounting · Weevil

Introduction

The West Indian sweetpotato weevil, *Euscepes postfasciatus* (Fairmaire), is a serious pest of sweet potatoes. Infested roots induce the production of a terpenoid, ipomeamarone, which may make even slightly damaged roots inedible to humans and animals (Akazawa et al. 1960). Therefore, even low weevil densities can cause high crop losses and prevent trade. The species originate in the Caribbean Island region, but its distribution has now expanded widely throughout South America and the Pacific islands (e.g., Sherman and Tamashiro 1954; Chalfant et al. 1990; Raman and Alleyne

1992). In Japan, this species is an invasive pest and is widespread throughout the Ryukyu Islands (Okinawa Prefecture) and the Amami Islands (Kagoshima Prefecture) in Japan (Yasuda and Kohama 1990; Moriya 1997). Sweet potatoes cannot be exported from these islands, where it occurs, due to the Plant Protection Law of Japan.

Sterile insect technique (SIT) is an environmentally friendly pest control technique that is applied in the integrated, area-wide control of major pests (e.g., Dyck et al. 2005; Koyama et al. 2004). It can be used to suppress, contain, or eradiate introduced and native populations and to prevent establishment or re-establishment after eradication. In the southwestern islands of Japan, another weevil pest exists, *Cylas formicarius*, an invasive species of weevil that attacks sweet potatoes in the same way as *E. postfasciatus* (Kumano 2014; Moriya 1997; Moriya and Miyatake 2001; Yasuda and Kohama 1990). Therefore, SIT was applied to *C. formicarius* and eradication of this species was achieved on Kume Island in 2012 (Himuro et al. 2022a, b) and Tsuken Island in 2021 (Ikegawa et al. 2022). *C. formicarius* has a sex pheromone that strongly attracts male, and thus the

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pheromone initially reduced the density of males in the field with a male annihilation technique (MAT), and thereafter sterile weevils were released for eradication (Himuro et al. 2022a, b).

However, the absence of strong volatile attractants for *E. postfasciatus* makes it difficult to eradicate the pest from the islands using SIT. LED light traps of this species are currently being used for monitoring, but the attraction rate is not high (Nakamoto and Kuba 2004). Because SIT aims to eradicate the pest through mating of the target insect, information on the distribution of the target species on host plants and on the sites where courtship and mounting (including mating) behavior occur would be useful to eradicate it.

Previous studies of *E. postfasciatus* have investigated irradiation methods for sterilization and the mating competitiveness of sterile weevils (Kumano et al. 2008), rearing methods (Shimoji and Yamagishi 2004; Ohishi et al. 2018), insect quality control for mass-reared insects (Shimoji and Miyatake 2002; Himuro et al. 2018; Misa et al. 2020), LED traps that attract insects (Nakamoto and Takushi 2001, 2002; Nakamoto and Kuba 2004; Katsuki et al. 2012), mating behavior (Himuro et al. 2017, 2021, 2022a, b; Sato and Kohama 2007; Kumano et al. 2008, 2009c, 2010, 2011), and dispersal ability in fields (Kinjo et al. 1995; Kumano et al. 2009a, b, c).

Knowledge of the distribution of their diurnal variation and egg-laying and mating behavior on host plants in the field will provide crucial insights into an effective SIT to eradicate this weevil. Tsurui-Sato et al. (2019) examined the distribution of males and females on sweet potato tuber roots, and it would be important for SIT, which eradicates target pests via mating, to examine the distribution of males and females in the above-ground areas of sweet potatoes in the fields where they are active. They conducted indoor tests on the effect of the male presence on the spatial distribution of males and females of *E. postfasciatus* using sweet potato tubers, and found that the spatial distribution of females and males was altered in this species by manipulation of the presence or absence of the opposite sex. In Tsurui-Sato's experiment (Tsurui-Sato et al. 2019), the tubers of the sweet potato were exposed, but in general, the tubers are buried and the stems and leaves are above the ground. In the present experiment, therefore, we used sweet potato seedlings to examine the diurnal distribution of females and males of *E. postfasciatus* on the seedlings, the effect of the presence of one sex on the distribution of the other sex, the plant part where mounting behavior occurs, and distribution of eggs laid on the seedlings. It is very important to know how weevils are distributed on the stems and leaves to control them.

Females of *E. postfasciatus* lay eggs mainly at night by puncturing the host plant with the proboscis, and after laying eggs, females cover the eggs with feces (Raman and Alleyne 1992; Shimoji and Kohama 1994). The eggs laid on the host

plant can, therefore, be confirmed visually and by host dissection. Females of this weevil tend to lay eggs preferentially on roots within the first 2 cm above soil surface (Raman and Alleyne 1992). Whether this property is due to the insect's sense of verticality or to the characteristics of the seedlings themselves remains to be elucidated, and this is important for clarifying the ecology of this species. Therefore, we also examined the distribution of females and egg sites when the seedlings were placed upright and upside down.

Materials and methods

Insects and seedlings

Sweet potato seedlings were sprouted indoors from sweet potato tubers and grown to 8 leaves (20–30 cm tall) as shown in Fig. 1. The leaves of the seedlings were numbered 1–8 from the top, with 1–4 being the upper and 5–8 the lower. Each seedling was placed in a glass vial (50 ml, 40 mm × 78 mm) full of water, the mouth sealed with Parafilm, and placed in the center of a plastic tray (27 × 37 cm, 12 cm height). The edges of the trays were coated with talcum powder to prevent weevils from escaping. Seedlings
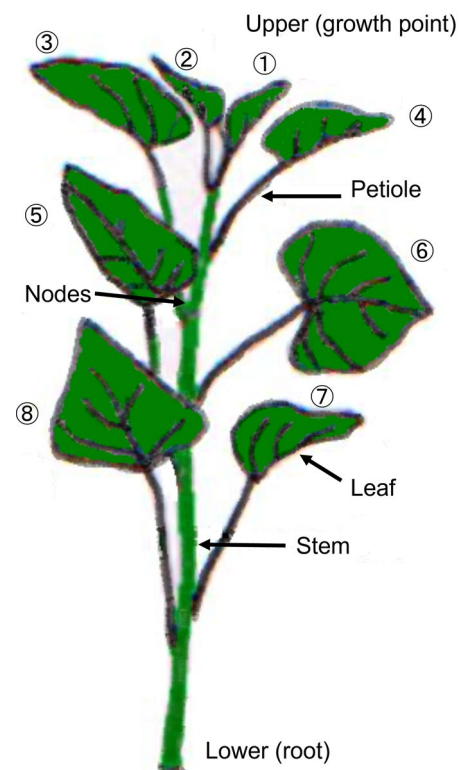

Fig. 1 Sweet potato seedlings used in the experiment with the names of each part. The leaves of the seedlings were numbered **1**–**8** from the top, with **1**–**4** being the upper and **5**–**8** the lower

were divided into five parts: leaves, petioles, nodes, stems, and outside (see Fig. 1). Places other than on the seedlings, such as on the tray, were considered outside.

E. postfasciatus weevils were derived from about 1,500 adults hatched from damaged sweet potatoes collected in Gushichan Village, Okinawa Prefecture, in May 2000 and reared cumulatively for about 7 years using sweet potato tubers at the Okinawa Prefectural Plant Protection Center. Pupae were picked up from sweet potato tubers to obtain adult weevils of approximately the same age for use in the experiment. Pupae were kept in plastic petri dishes (9 cm width and 1 cm height) lined with filter paper, and adults were separated into males and females by the method of Yasuda and Naito (1991) one to two days after hatching. Thereafter, fresh sweet potato tuber pieces as food were supplied twice a week until adults were used for observation. The weevils were reared in a room which was kept at a constant 28 °C and a controlled day length of 14L–10D.

Experiment 1. Distribution of adults on sweet potato plants

Five unmated females (28–30 days old, virgin) were released onto the stem in the middle of the prepared seedlings (Fig. 1) at 10:00 a.m. on the day the experiment was started, and observation began one hour later at 11:00. Weevil locations were recorded every two hours starting at 11:00 a.m., one hour after the adults were released. Twenty-four hours later, five unmated male adults were released on the stem in the middle of the seedlings, and their distribution was observed every two hours for 48 h in total.

In addition to this, an experiment was conducted in which the order in which males and females were released was changed. Five unmated male adults were released at 10:00 on the first day of the experiment, five additional unmated female adults were released 24 h later, and adult distribution was observed every two hours for 48 h.

After releasing individuals of both sexes, we also noted where the mounted individuals were also covers this. To distinguish males and females, we pre-marked the backs of males and the heads of females using white markers (quickly drying paints, Mitsubishi Paint Marker). During the dark period, observations were made under red light by turning on a light with a red filter attached to a flashlight so as not to interfere with the weevil's behavior. The number of mounts was counted because it was not possible to confirm whether or not they were mating. The experiment was conducted with eight replicates, in four of the eight replicates the females were released first and the males later, while in four replicates the males were released first and the females later.

Experiment 2. Distribution of adults on seedlings turned up and down

The potato seedlings were turned upside down, five unmated or mated females were released on the stem in the middle of the seedlings, and their distributions of adults on the seedlings and the eggs laid on seedlings were checked. To check the eggs, we first visually checked the lid of the eggs and feces. Some eggs were completely covered, so we removed the lid, removed the eggs with tweezers, and counted them.

We prepared normal seedlings with the growth part on the top and the root part on the bottom, and conversely, inverted seedlings with the growth point on the bottom and the root side on the top (see Fig. 5). The leaves of these seedlings were designated as 1–8 from the growth point side (see Fig. 1), with the four from the growth point (1–4) side being the 'upper side' and the fifth to the eighth being (5–8) the 'lower side' in the normal seedlings. In the inverted seedlings, the 5th to 8th leaves (5–8) and the 1st to 4th leaves (1–4) were considered as the upper and lower sides, respectively. The vertical distribution of females and position of eggs laid on the seedlings were recorded. We prepared 8 seedlings in total. The experiments were replicated two times for each trial, 1st trial: 8 for unmated females and 2nd trial: 8 for mated females. The numbers of eggs released were 5 for mated females per seedling and 5 for unmated females per seedling, respectively. Total numbers used were 40 mated and 40 unmated females. The number of insects used (5 unmated and 5 mated) and the number of experimental repetitions (16 seedlings and 8 repetitions) were arbitrary, considering the numbers to satisfy statistical significance.

Statistical analysis

Because the same individuals were targeted for measurement each time, analyses were conducted separately each time. In each treatment, data on the percentage of individuals that were on the plant were analyzed by a generalized linear model (GLM) with logistic regression analysis of binomial distribution, and sex as an explanatory variable. GLMs were used to test data during first 24 h and after 24 h, respectively. In each treatment, data on the number of individuals per plant site at each time were analyzed with a generalized linear mixed model (GLMM) with binomial distribution, and plant site, sex, and interaction between plant site and sex as explanatory variables, and replication of experiment as a random effect. In each treatment, data on the number of mounting pairs at each time were analyzed by GLMM with binomial distribution, and plant site, sex, and interaction between plant site and sex as explanatory variables, and replication of experiment as a random effect. Comparison of the numbers of eggs laid per oviposition site was analyzed

by the Wilcoxon signed rank test. These analyses were conducted using R ver. 4.1.0 (R Core Team 2021).

Results

Experiment 1. Distribution of adults on sweet potato plants

Figure 2 shows distributions of weevils on plants at each time, and Supplementary Tables 1 to 3 show results of statistical analysis of these data. There were significant differences in the numbers of weevils at some time points (Supplementary Tables 1–3). In the two experiments, most of the males and females were distributed on the plants in the daytime, while at night, females especially stayed away from the plants in large numbers (Fig. 2, Supplementary Tables 1–3). When only females were released first, observation began at 11:00 a.m. and many females were found off the plant between 13 and 19 h (Fig. 2, Supplementary Tables 1, 2). At 23:00 most females had returned on the plant (Fig. 2,

Supplementary Tables 1, 2). On the other hand, when only males were released, the males remained mostly on the plant during both nighttime and daytime (Fig. 2, Supplementary Tables 1, 3). Even after cohabitation of males and females for 24 h, about half of the females were found off the plants during the nighttime, but most of the males were found on the plants (Fig. 2, Supplementary Tables 1, 3).

Figure 3 shows in detail the distribution of females and males by parts of the seedling during the observation period, and Supplementary Tables 4–6 show results of GLMM for these data. There were significant differences in the number of weevils at some time points (Supplementary Tables 4–6). Many individuals were present on leaves at first, and then both sexes moved to nodes of the plant during the dark period. During the daytime, many individuals of both sexes left the nodes, and when at lights were off again, they moved to the leaf, petiole, stem, or surface (outside) of the plant (Fig. 3, Supplementary Tables 4–6). These data indicate that this species is nocturnal and is abundant in plant nodes during the day, but females in particular move around at night on petioles, stems, and away from the plant.
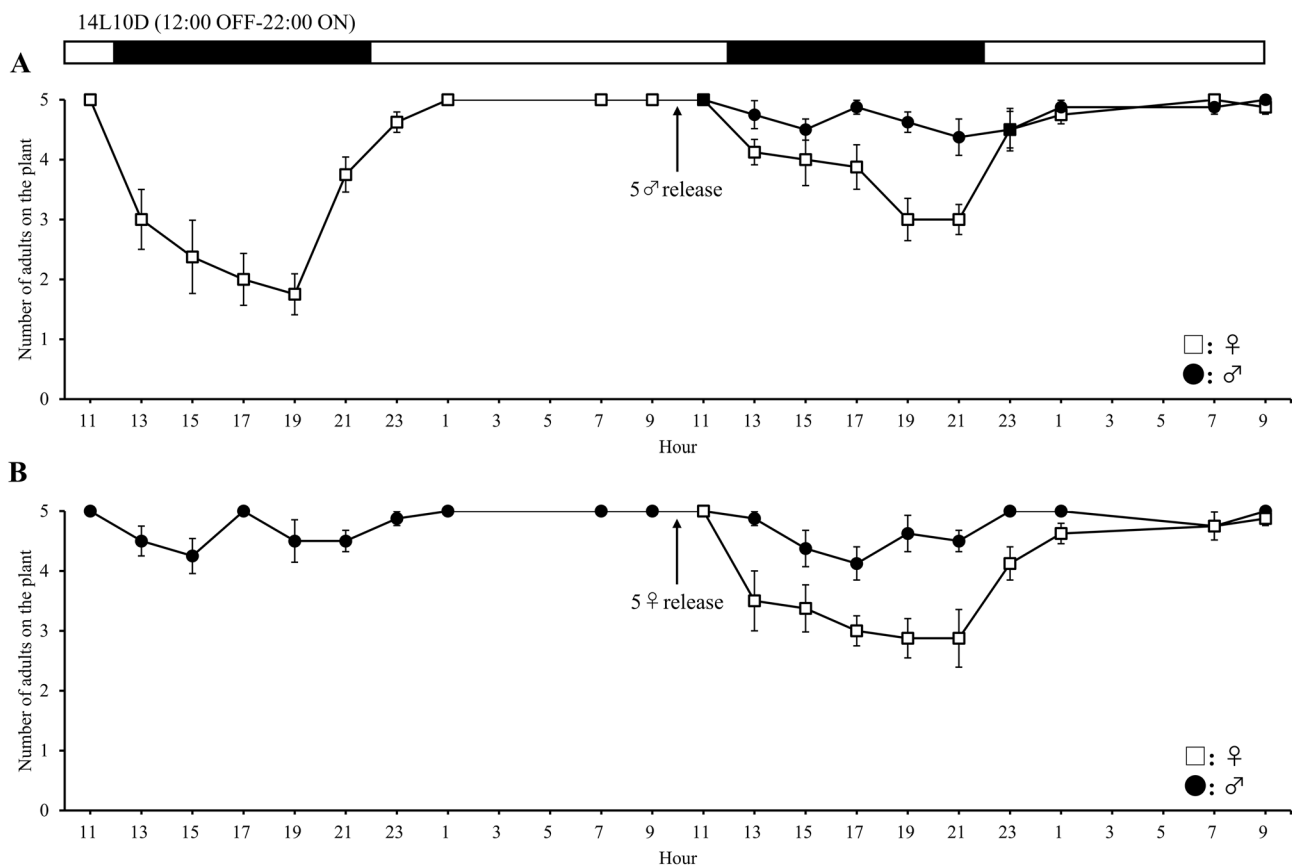

Fig. 2 Numbers of adults distributed on or off the seedlings each time. Closed and open circles show males and females, respectively. Each bar shows the standard error. Dark periods start from 12 and end at 22 h (14L10D). **A** an experiment in which females were released first and males were released 24 h later; **B** an experiment in which males were released first and females were released 24 h later. The arrows indicate the time they were put in

Fig. 3 Numbers of adults distributed on the seedlings each time. Closed and open circles show males and females, respectively. Each bar shows standard errors. Dark periods start from 12 and end at 22 h (14L10D). **A** an experiment in which females were released first and males were released 24 h later; **B** an experiment in which males were released first and females were released 24 h later. Refer to Fig. 2 for timing of additional male or female inputs
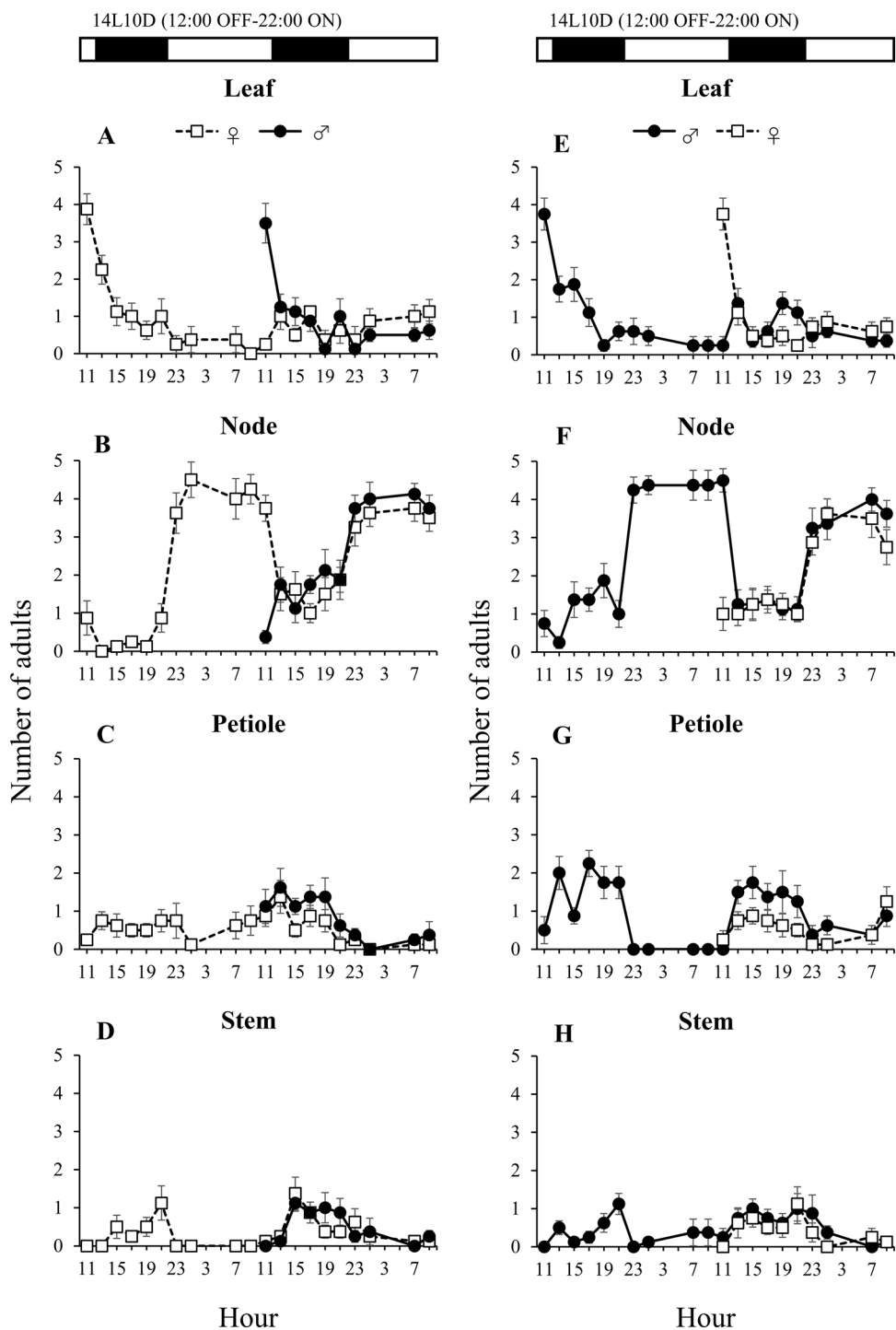

Figure 4 shows the locations where mounting behavior was observed in the experiment when females were released first and males were released 24 h later and when males were released first and females were released 24 h later, and Table 7 shows results of GLMM for these data. There were significant differences in the number of mountings at some time points (Supplementary Tables 7). Regardless of which sex was released first, mounted individuals that remained on the plant were found most frequently in the nodes (Fig. 4, Supplementary Tables 7).

Experiment 2. Distribution of adults on seedlings turned up or down

Figure 5 shows the distribution of unmated and mated females when the seedlings were placed normally (Fig. 5A,

Fig. 4 Number of pairs observed in mounting behavior on seedlings by time: black bars indicate the results of the experiment in which the female was released first, and white bars indicate the results of the experiment in which the male was released first. Each bar on graphs shows standard errors
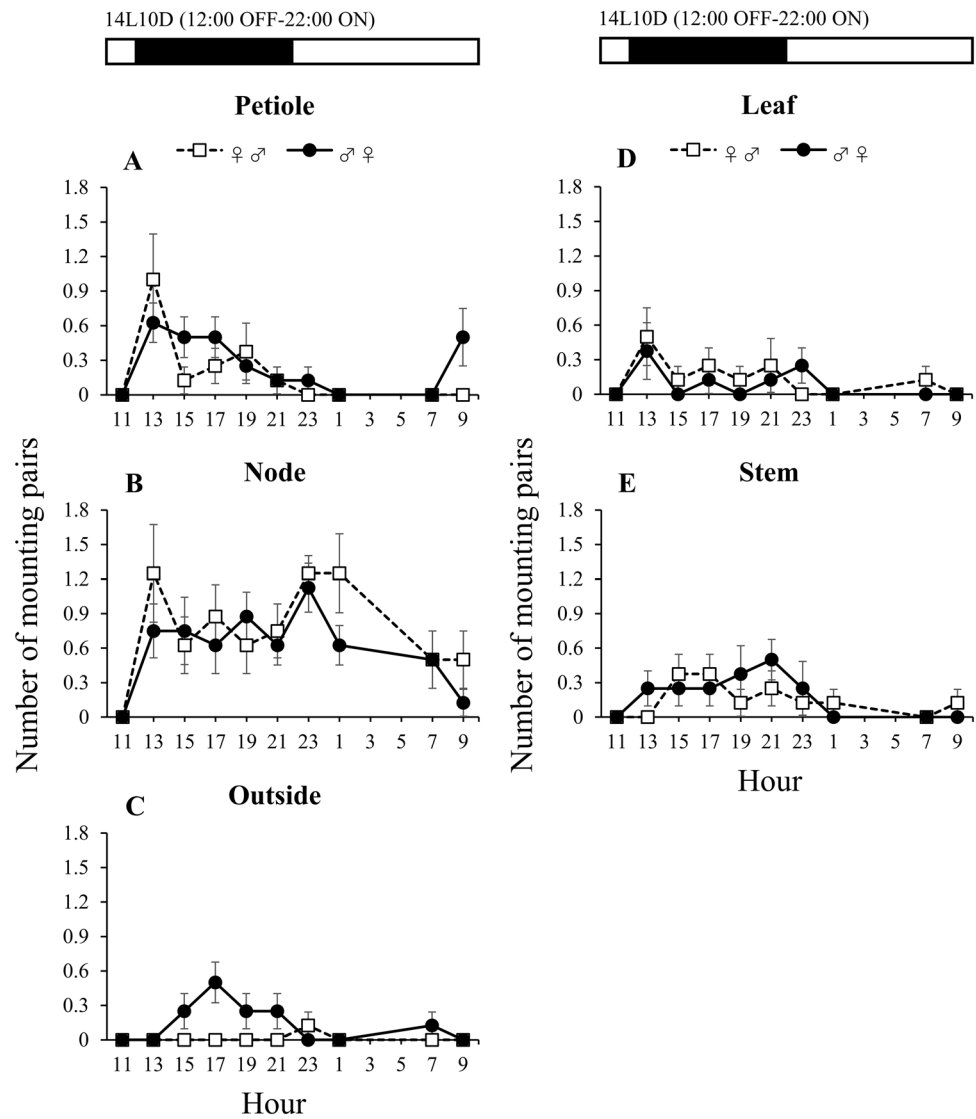
B) and when the seedlings were upside down (Fig. 5C, D). The Wilcoxon signed rank test ($P < 0.05$) showed a significant difference in the distribution of unmated and mated females when the seedlings were placed normally, except at 11:00 and at 17:00 (see Fig. 5A, B). When the seedlings were placed upside down, females were mainly distributed on the upper growth part of the seedlings (at the base), but there was no significant difference between unmated and mated females except at 11:00 (see Fig. 5C, D). The results indicate that mated females of *E. postfasciatus* clearly prefer to locate on the root side of the seedlings. We thought that this factor might be related to the oviposition location and, therefore, we investigated the number of eggs laid on these seedlings.

A comparison of the numbers of eggs laid per oviposition site is shown in Table 1. The mean number of eggs laid on the upper growth point side on normal seedlings was 0.33, and significantly more eggs were laid on the lower root side

(7.17), with more than 95% of the eggs on the root side ($p = 0.0171$, Table 1). In contrast, when the seedlings were upside down, significantly more eggs were oviposited on the root side (12.43) than the lower root side, even though the root side (1.00) was on top ($p = 0.0458$). These results indicate that mated females oviposit more on the root side of the seedlings, regardless of their vertical position at the base of the seedlings, and that their behavior of locating more frequently at the root part in the earlier test is related to their egg laying behavior.

Discussion

Unmated males of *E. postfasciatus* were well distributed on the host plant during the daytime and at night, but females left the plant at night and were often found off the plant (Fig. 2). Although there was no difference in distribution

Fig. 5 Proportions of positions on the seedlings where females were distributed when the seedlings were placed normally (**A** and **B**) and when they were placed upside down (**C** and **D**), for each observation period. Dark periods start from 11 and end at 22 h (14L10D). **A** and **C** show the distribution of unmated females, and **B** and **D** show the distribution of mated females
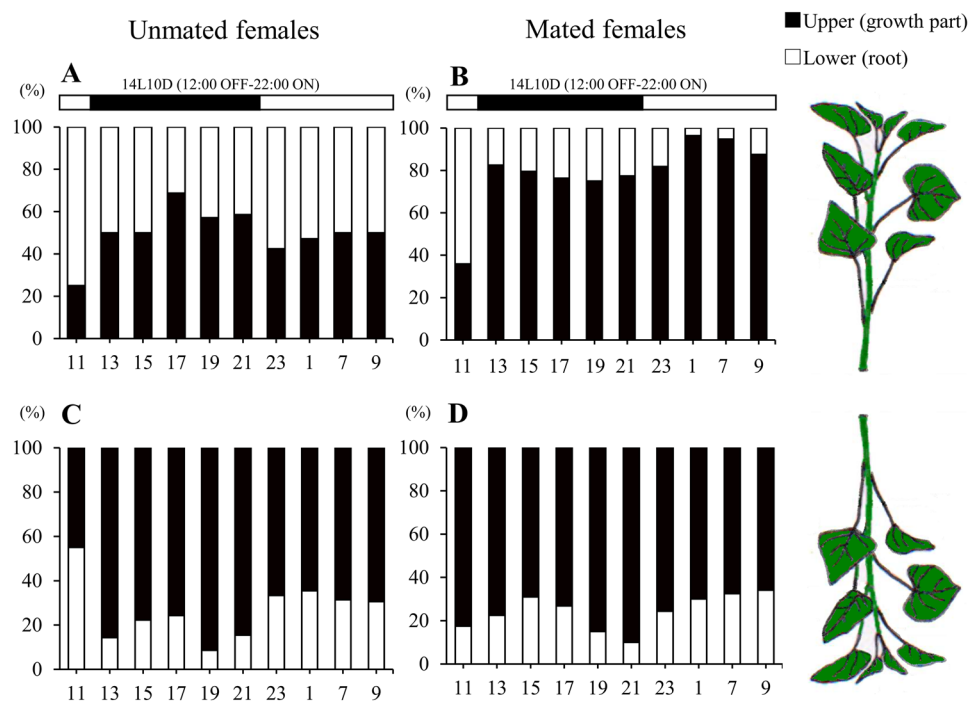

Table 1 Comparison of mean number ($\pm$ SD) of eggs laid on normal and upside-down seedlings

	Normal seedlings			Upside-down seedlings		
	Side	Mean $\pm$ SD	%*	Side	Mean $\pm$ SD	%*
Upper	Growth point	0.33 ± 0.82	4.4	Root	12.4333 ± 4.39	92.6
Lower	Root	7.1733 ± 4.40	95.6	Growth point	1.0033 ± 1.53	7.4
**p-values		0.0171			0.0458	

*(Number of eggs laid on the top or bottom side of seedlings/total eggs laid)$\times$100

**Wilcoxon signed rank test (8 replications)

when both sexes were present at the same time compared to the distribution of males only, females tended to stay at the nodes on the plant during the dark period more than when they were present without males (Fig. 2). Tsurui-Sato et al. (2019) released males and/or females on sweet potato tuber roots and found that females spent significantly more time on sweet potato tuber roots than males. On the other hand, the present results showed that whether males were released first or females first on the seedlings, females were more likely to stay away from the seedlings at night, whereas males were always on the seedlings (Fig. 2). Tsurui-Sato et al. (2019) also found that when males and females were released simultaneously, the probability of males staying on the sweet potato tubers was significantly higher in populations with cohabiting females than in populations with only males, and females tended to stay on the sweet potato tuber when males were present. Regarding this result, Tsurui-Sato et al. (2019) reported that female distribution patterns are affected by the presence of males, possibly due to males imposing costs on

females through sexual harassment. However, the present results showed that females, not males, left the seedlings at night, both when females were alone and when they were cohabitated with males (Fig. 2). The differences in the distribution pattern of the sexes in the two studies may be due to differences between sweet potato tuber roots and seedlings, or to differences in density on the host of released males and females. In the previous study (Tsurui-Sato et al. 2019), the tubers of the sweet potato were exposed for *E. postfasciatus* for the adults, but in general, the tubers are buried and the stems and leaves are above the ground. It is very, therefore, important to know how weevils are distributed on the stems and leaves to control them. This is the difference from previous studies and a very important value of the present result. Further investigation of the distribution of the sexes of *E. postfasciatus* on plants will be necessary in the field.

In the present study, we found the distribution of adults by site of seedlings also differed by time of day, with the majority of both sexes distributed on the node of the seedlings at

night (Fig. 3). In addition, a higher proportion of mounted pairs (including mating pairs) were found at the nodes of the plant body (Fig. 4), suggesting that the nodes have much to do with mounting behavior. The ecological reason mounting pairs of this species are often observed in the node of seedlings is unknown, although there is a possibility that it may be harder to be found by natural enemies. Besides avoiding predation, other reasons might be, for example, that males are less likely to take females from other males (Blum and Blum 1979), or that females are less likely to be sexually harassed by other males (Arnqvist and Rowe 2005). It is necessary to investigate the reason in the future.

Previous studies on locomotion in this species have reported sexual differences in adults (Shimizu and Moriya 1996a, b). Females exhibit higher locomotion activity, longer walking distances and walking times, and faster walking speeds than males (Shimizu and Moriya 1996a). Data comparing the locomotor activity of *Cylas formicarius* and this species show that both species are more active in the dark than in the light period (Shimizu and Moriya 1996b). Very interestingly, however, *C. formicarius* males dispersed further than females, while in *E. postfasciatus* no significant difference was reported in walking activity between females and males, although females tended to have higher activity than males (Shimizu and Moriya 1996b; Kumano et al. 2009b). Combined with the present results, it is likely that *E. postfasciatus*, a nocturnal species, has a behavioral pattern in which females, rather than males, move. This inference is very important when considering how the mating system of this species affects the sterile insect technique (SIT) because SITs depend on the mating of released males with wild females.

Emlen and Oring (1997)'s classic study showed that female dispersal is strongly dependent on the dispersal of resources (food, shelter, egg-laying sites, etc.), and male dispersal is dependent on female dispersal (Shuster and Wade 2003). Because the present study examined the distribution of the sexes in the limited space of a tray, the females can return to the seedlings. Females may move more in the open field where there are no restrictions on movement. In general, female dispersal is common in species where males defend resources (e.g., Choe and Crespi 1997; Miyatake 2002). The mating system of *E. postfasciatus* has not been studied at all. The results obtained in this study, which basically show that females disperse at night (see Shimizu and Moriya 1996a, b), and together with previous studies showing distribution patterns of females and males on sweet potato tuber roots (Tsurui-Sato et al. 2019), the present results provide new information on the invasion risk and control of this species. Both the previous study (Tsurui-Sato et al. 2019) and the present study were conducted in the laboratory, suggesting that future field studies on the distribution patterns of males and females of this species are needed.

The sterile insect technique applied to control this species is a method of eradicating the pest by having sterile males seek out and mate with females in the field, taking advantage of the fact that the eggs laid by the wild females do not hatch (e.g., Koyama et al. 2004; Dyck et al. 2005). Therefore, it is important to know the distribution of wild females and males in the field. Many fruit fly species that have been eradicated by sterilization methods have been found to have lek mating systems in the field (Iwahashi and Majima 1986). Identification of where infertile males mate in the field has been important data to support the sterilization method (Hibino and Iwahashi 1991). However, it was not known for *E. postfasciatus* in what locations courtship behavior occurs. It should also be noted that theoretical studies (Ikegawa et al. 2021) suggest that the mating systems of fruit flies and weevils are different.

The study also found that adults of *E. postfasciatus* are frequently present at the nodes of the plant and also prefer to locate and lay eggs at the base (root parts) of the seedlings. Adults may obtain signals from plants to recognize specific egg-laying sites (also see Nakamura et al. 2011). The present results suggest that the root side of sweet potato seedlings is particularly likely to have substances that attract mated females and that contain a high amount of egg-laying substrate. Combined with the high distribution of mated females at the nodes, the data from the present study may be helpful in the search for egg-laying attractants in *E. postfasciatus*.

In the present experiment, we used a mass-reared strain of *E. postfasciatus* that had been maintained for many generations without host plants other than tuberous roots. Therefore, it should be noted that these mass-reared insects may have traits more adapted to indoor living than wild insects (see Miyatake 1998). It is considered necessary to conduct similar experiments with wild weevils in the future.

In conclusion, we found the following three results: (1) during the day, both sexes of the West Indian sweetpotato weevil, *E. postfasciatus*, remain in the nodes of the seedlings and do not move, (2) mounting behavior occurs at a node during the night, and (3) even when the seedlings were placed upside down, eggs were found near the seedling roots. The results, therefore, will contribute important basic data for the application of the Sterile Insect Technique against this species.

Declarations

Conflict of interest We declare that we have no competing interests.

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