

Pattern of immigration of the sorghum plant bug *Stenotus rubrovittatus* (Hemiptera: Miridae) into paddy fields from a large source habitat

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Abstract Evaluation of the landscape-level movement of *Stenotus rubrovittatus* (Matsumura), a major rice pest in Japan, is essential for establishing management strategies. We assessed the immigration timing and the average dispersal distance from a bank slope covered with Italian ryegrass *Lolium multiflorum* Lam. to paddy fields by periodic sampling in two regions in Chiba Prefecture. The immigrant densities in paddy fields increased exponentially as they approached the bank slope as a large-scale habitat

of the insect. The relationship between immigrant density and distance from the source habitat fit an empirical model and theoretical model well. The theoretical model estimated the average dispersal distance during immigration: that of females was 72.0 and 92.1 m and that of males was 122.0 and 112.9 m in the respective regions. In addition, the average dispersal distance of males increased 7 days or later after the rice heading date despite the steady dispersal distance of females.

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Introduction

Insects are constantly moving at various scales, such as from crop fields to non-crop fields or from one plant to another. Non-crop plants such as weeds, either inside or outside crop fields, serve as alternative hosts (Fleischer et al. 1988; Horton et al. 1988), overwintering sites (Cleveland 1982; Negrón and Riley 1991), and oviposition sites (Boivin and Stewart 1983; Busching and Turpin 1976) for both insect pests and their natural enemies. Thus, it is well known that there are close interactions between insects in crop fields and those in non-crop habitats (Norris and Kogan 2000). Much knowledge about host manipulation of control pests has been gathered (e.g., Fleischer et al. 1988; Panizzi 1992). Removal of non-crop vegetation around fields has been regarded as an important cultural factor in integrated pest management (IPM) (Coaker 1987). IPM programs can in theory be nested by scale; for example, field < cropping system < landscape < ecoregion. Therefore, understanding how, when, and where insects move is a key component of habitat manipulation

strategies at all scales. It also helps the development and deployment of regional-scale IPM programs (Irwin 1999).

The sorghum plant bug, *Stenotus rubrovittatus* (Matsumura), is a principal pest of rice, *Oryza sativa* L., in Japan, causing pecky rice (kernel spotting) (Higuchi 2010). It usually breeds and overwinters on heads of gramineous plants in grassy fields or meadows, and migrates to paddy fields just after rice heading (Hayashi and Nakazawa 1988). Weed removal can decrease damage (Teramoto 2003), because the pest population and damage to rice plants can be influenced by non-crop vegetation within and near paddies (Kashin et al. 2009; Ono et al. 2007).

The area of *S. rubrovittatus* infestation has expanded throughout Japan in recent years (Higuchi 2010; Watanabe and Higuchi 2006). One reason seems to be increases in the abandonment of paddy cultivation and in meadows where host plants, mainly annual or biennial gramineous plants typified by Italian ryegrass *Lolium multiflorum* Lam. and *Digitaria ciliaris* (Retz.) Koeler, are dominant (Ito 2004; Niiyama 2000). Takada et al. (2000) broadly separated paddy fields into categories by their conditions of surrounding source habitats of *S. rubrovittatus*. They reported that the density and damage of *S. rubrovittatus* were higher in paddy fields close to the large source habitats with mainly Italian ryegrass than in those that had weeds only in the field boundaries. Ecological studies recently began on landscape areas where *S. rubrovittatus* and its source habitat interact each other (Yasuda 2012; Yasuda et al. 2011; Yoshioka et al. 2011). These reports suggest that the habitat manipulation strategy of this pest needs to be developed from the viewpoint of the landscape or areawide scale, not just of individual paddy fields. Although fundamental understanding of the movement of a pest is a key constraint to developing and deploying larger scale IPM programs (Irwin 1999), little is known about its movement pattern in the field. Here, we analyzed the immigration period and dispersal distance of *S. rubrovittatus* systematically by using the timing and distance data of its immigration from a large source habitat to paddy fields during the heading to grain-filling period of rice. Insect abundance dispersed from one source is indicated by some equations that have distance as a parameter (Taylor 1978). Kobayashi (2007) reported the flight ability of *S. rubrovittatus* was different between sexes. We hypothesized that immigration

timing and flight distance are influenced mainly by the distance from a large source habitat to paddies and also by the sex of *S. rubrovittatus*. We fitted the immigrant density in paddy fields to an empirical model and a theoretical model, and tried to analyze the dispersal pattern from source habitat to paddy fields.

Materials and methods

Field sampling

Insects were sampled from early July to mid-August in paddy fields in the Kozaki region (35°54'N, 140°23'E) in 2008 and the Sanno-wakeme region (35°53'N, 140°35'E) in 2009 in Chiba Prefecture, Japan (Table 1). These regions are located in alluvial lowlands of the Tone River and, at the time of the study, comprised homogeneous paddy fields adjacent to belt-like bank slopes (Fig. 1). These bank slopes were covered with grasses, mainly Italian ryegrass, an important host plant for *S. rubrovittatus* (Hayashi 1986); *S. rubrovittatus* occurs frequently on these grasses (Katase et al. 2007; Takeda et al. 2008, 2011). We regarded the bank slopes as the main source of the *S. rubrovittatus* captured in the paddy fields, because there were no other large source habitats nearby.

Sampling site details are shown in Table 1 and Fig. 1. A minimum distance of 10 m to the borders of the field was used for sampling, and each sampling site was 20 m or more apart from other sites. The shortest distance from sampling sites to the bank slope was calculated using ArcGIS version 9.2 (ESRI 2004).

Adult *S. rubrovittatus* were caught around each sampling site by 20 sweeps with a 36-cm-diameter insect net on a 120-cm-long handle. Sampling was performed twice a week from 2 weeks before the predicted heading date to just before harvest. Heading dates are defined as when heading was observed in 40–50 % of hills.

Immigration period and sex differences

We analyzed how immigration of *S. rubrovittatus* was influenced by the distance from the source habitat and sex. For such analyses, empirical equations have been

Table 1 Overview of sampled paddy areas

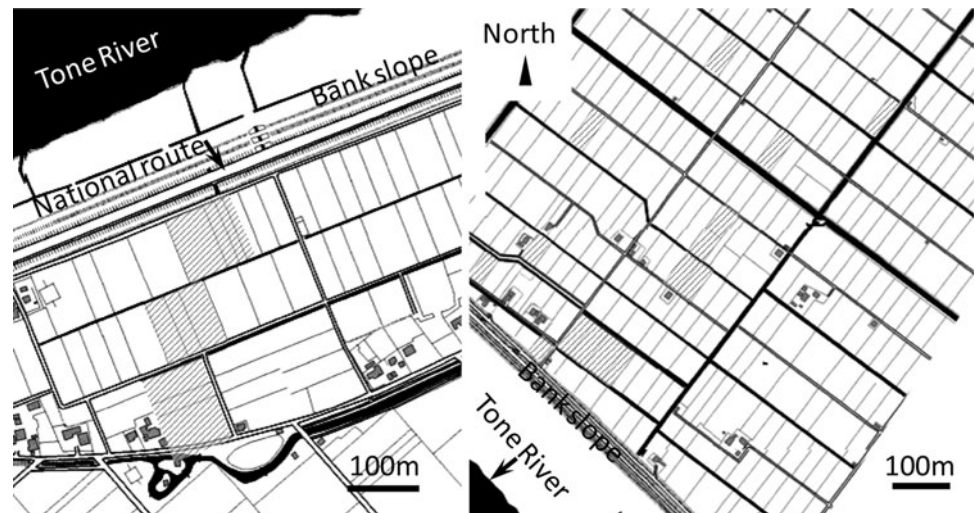
Region ^a	Latitude/longitude	Cultivar	Year	No. of sampling sites	Sampling range (m) ^b	Heading date ^c
Kozaki	35°54'N/140°23'E	Koshihikari	2008	18	290	4 August
Sanno-wakeme	35°53'N/140°35'E	Akitakomachi	2009	12	750	13 July

^a The paddy areas adjacent to a bank slope along the Tone River, Chiba Prefecture

^b To the farthest sampling point from the bank slope

^c Heading dates are defined as when heading was observed in 40–50 % of hills

Fig. 1 Locations of paddy sampling sites in Chiba Prefecture, Japan. Hatching shows paddy fields sampled. *Left* Kozaki region; *right* Sannowakeme region



advocated. Taylor (1978) showed that the following equation, proposed by Wallace (1966), was appropriate:

$$\log y = a + b\sqrt{x} \tag{1}$$

where y = abundance, x = distance from the source, and a and b are constants. We added sex as another predictor variable and log-transformed the number of adult *S. rubrovittatus* captured at 0, 3, 7, 10, 14, 17, and 21 days after the heading date (DAH) as the response variable ($\log(y + 1)$).

We used multivariate analyses of variance (MANOVA) because the response values were collected periodically at the same location. In the design matrix for the multivariate comparison (Eq. 2), the columns indicate the variables themselves, and the rows indicate the combinations of variables to compare. Equation 2 shows a comparison between numbers captured on one date and on the following date (for example, 3 and 7 DAH):

$$\begin{bmatrix} 1 & -1 & \dots & 0 & 0 \\ \vdots & & \ddots & & \vdots \\ 0 & 0 & \dots & 1 & -1 \end{bmatrix} \tag{2}$$

If MANOVA showed that sex or distance had a significant effect on abundance, we performed separate analyses by sampling date to determine when the changes occurred. The level of significance was 0.007 ($0.05 \div 7$ sampling dates). These analyses were performed in JMP v. 10.0.0 software (SAS Institute Inc., Cary, NC, USA).

Dispersal distance

We compared the average dispersal distances between males and females. Yamamura et al. (2003) described the average dispersal distance ($1/\sqrt{\lambda_D}$) as a parameter in one-dimensional (1D) space (Eq. 3):

$$f(x) = \frac{n_0}{2} \sqrt{\lambda_D} \exp(-|x|\sqrt{\lambda_D}) \tag{3}$$

where n_0 = the number of individuals released, x = the distance at which they settle, $\lambda_D = \lambda/D$, where λ = the rate at which individuals settle at a position, and D = the diffusion coefficient, which measures the dispersal rate (distance²/time).

Yamamura et al. (2003) developed Eq. 3 by releasing marked individuals at a single moment and capturing them continuously in pheromone traps. We considered our experiment to be equivalent to the model of Yamamura et al. (2003), because there was only one source in an otherwise empty area: a paddy field and pest individuals were invaded continuously there (Turchin and Omland 1999). Although Yamamura et al. (2003) defined a model in 2D space as well, we selected the 1D model because we considered the diffusion to occur vertically from the bank slope adjacent to the paddy fields.

We redefined Eq. 3 as:

$$g(x) = c \times \exp\left(-\frac{x}{d}\right) \quad (x > 0) \tag{4}$$

where $g(x)$ = the number of adults at the time when the effect of distance was significant, $c = n_0\sqrt{\lambda_D}/2$, and $d = 1/\sqrt{\lambda_D}$.

The parameters were derived by maximum likelihood estimation. The G-test examined the deviance of the model by Eq. 4 with the constant versus the empirical model Eq. 1, and rejection was at $p < 0.05$ significance based on a chi-squared distribution. These analyses were performed using R v. 2.13.2 software (R Foundation for Statistical Computing, Vienna, Austria) and the bbmle library (version 1.0.5.2) (Bolker 2012).

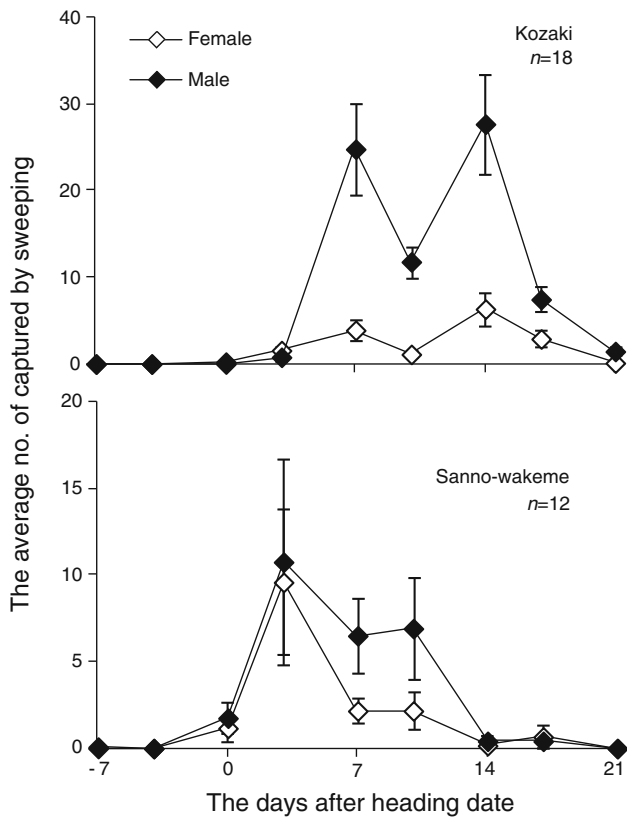


Fig. 2 Average numbers of adult *Stenotus rubrovittatus* captured by sweeping in paddy fields. Bars indicate SEM

Results

Immigration period and sex differences

In both regions of Japan, few adults were captured in the paddy fields before rice heading (Fig. 2). The density was high at 7 to 14 DAH in Kozaki and at 3 to 10 DAH in Sanno-wakeme (Fig. 2). It then dropped to near zero.

The density decreased clearly with the increase of distance from the bank slope at 7 and 14 DAH in Kozaki (Fig. 3) and at 3 DAH in Sanno-wakeme (Fig. 4). MANOVA showed that both distance and sex had significant effects on density in both regions, indicating these effects differed in their response over time (Table 2). Analyses by sampling date showed that distance had significant effects on density at 7, 14, and 17 DAH in Kozaki, and from 0 to 10 DAH in Sanno-wakeme (Table 3).

The number of males was significantly higher than that of females at 7–17 DAH in Kozaki, while being only 7 DAH in Sanno-wakeme (Table 3). Although significant differences between sexes were not detected at 10 DAH in Sanno-wakeme, more males were captured than females in an area within 100 m from the bank slope (Fig. 4). The patterns of the sex ratio were similar, but the number of males showed a tendency to be higher than that of females after 7 DAH.

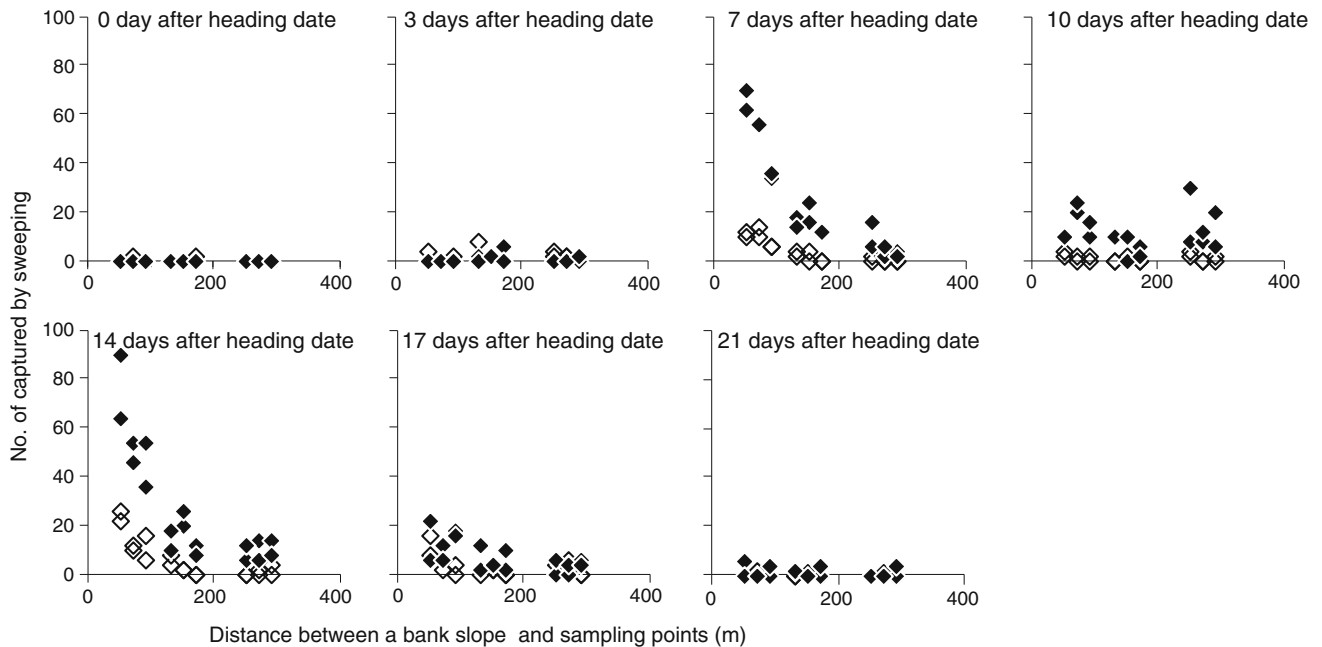


Fig. 3 Density distribution of adult *Stenotus rubrovittatus* in paddy fields in the Kozaki region. Void and black rhombuses indicate females and males, respectively

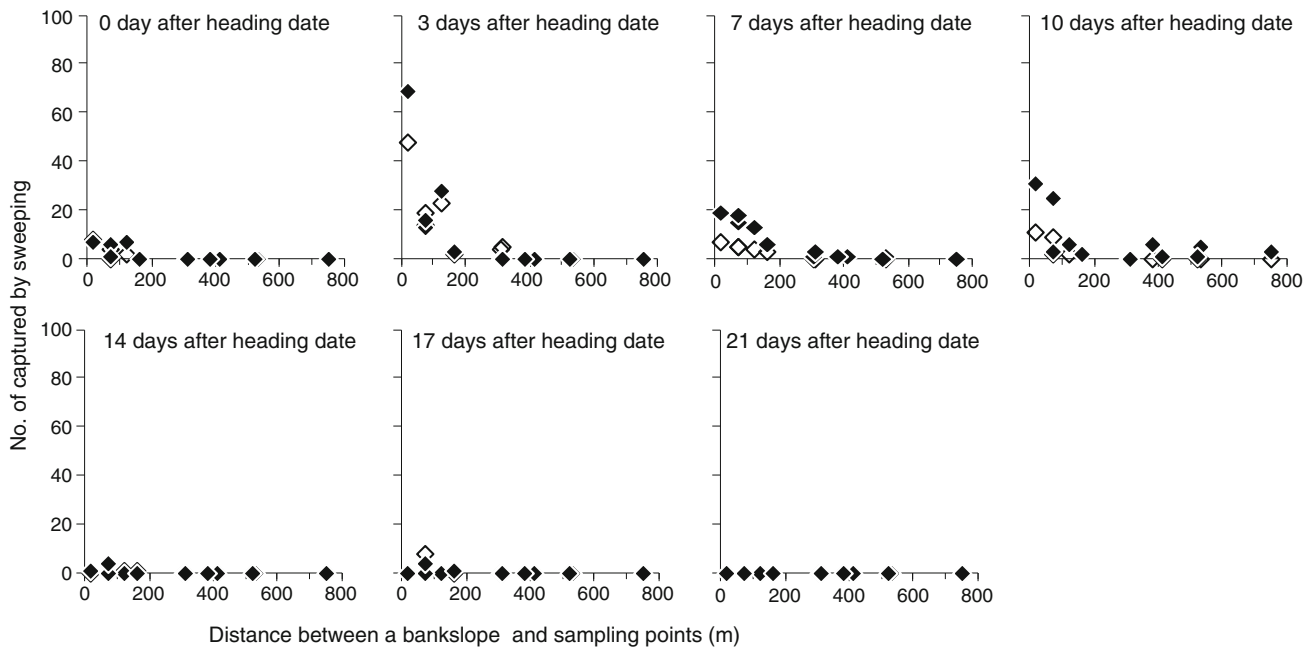


Fig. 4 Density distribution of adult *Stenotus rubrovittatus* in paddy fields in the Sanno-wakeme region. Void and black rhombuses indicate females and males, respectively

Table 2 Results of multivariate analysis of the numbers of *Stenotus rubrovittatus* collected

Region	Factor	df ^a	Exact F value ^b	p (Prob > F)
Kozaki	Whole model	12/56	15.67	<0.0001***
	Constant	6/28	45.11	<0.0001***
	Sex	6/28	22.10	<0.0001***
	Distance ^c	6/28	22.07	<0.0001***
Sanno-wakeme	Whole model	12/32	12.06	<0.0001***
	Constant	6/16	68.64	<0.0001***
	Sex	6/16	3.98	0.0130*
	Distance ^c	6/16	33.61	<0.0001***

The total number of adult *S. rubrovittatus* captured on seven sampling dates until 21 days after the heading date were log-transformed and fitted as multiple sequential responses

* $p < 0.05$, *** $p < 0.001$

^a Numerator/denominator degrees of freedom

^b The *F* value of the whole model is given by approximate *F*-test by Wilks' lambda

^c Square root of the distance between the bank slope and the sampling point (\sqrt{m})

Dispersal distance

The total numbers of adult *S. rubrovittatus* captured fit well to Eqs. 1 and 4 during the period in which the effect of distance was significant (7–17 DAH in Kozaki and 0–10 DAH in Sanno-wakeme). The curves obtained by the two

models were very similar (Fig. 5), with no significant differences (Table 4). Equation 4 gives the average distance of a captured male as 122.0 m in Kozaki and 112.9 m in Sanno-wakeme, and of that of a captured female as 72.0 and 92.1 m, respectively.

In Sanno-wakeme, the female dispersal distance remained steady from 3 DAH, whereas the male dispersal distance started smaller than the female dispersal distance and increased beyond it (Fig. 6).

Discussion

Although many previous studies reported that numbers of *S. rubrovittatus* adults peaked around 7 DAH and then decreased in rice paddies (Katase et al. 2007; Nakata 2000; Takeda et al. 2008), the immigration periods differed from 7 DAH in our experimental regions and varied between the regions. In Kozaki, the number of insects captured peaked at 7 and 14 DAH, and in Sanno-wakeme, it reached a peak at 3 DAH. Cultivars seemed to have less influence, because heading dates in Kozaki and Sanno-wakeme were similar to those in the other paddies. The immigration of *S. rubrovittatus* started and finished later in Kozaki than in Sanno-wakeme. The reason for this difference seems to be the different landscapes between the regions. In Sanno-wakeme, the paddy fields were directly adjacent to the bank slope as a source habitat. In Kozaki, a roadway, a non-habitat area, might delay the *S. rubrovittatus* invasion from the bank slope to paddies. Kikuchi et al. (2004)

Table 3 Parameters estimated by individual MANOVA of the numbers of adult *Stenotus rubrovittatus* captured

Days after heading date	Factor	Sanno-wakeme				Kozaki			
		Estimate	df ^a	F value ^b	p (Prob > F) ^c	Estimate	df ^a	F value ^b	p (Prob > F) ^c
0	Whole model		2/21	14.44	0.0001*		2/33	1.28	0.2906
	Constant	0.8350	1/21	43.13	<0.0001*	0.0723	1/33	1.10	0.3020
	Sex	-0.0342	1/21	0.47	0.5010	0.0265	1/33	2.09	0.1575
	Distance ^d	-0.0389	1/21	28.41	<0.0001*	-0.0037	1/33	0.47	0.4957
3	Whole model		2/21	50.87	<0.0001*		2/33	1.22	0.3072
	Constant	1.9464	1/21	172.10	<0.0001*	0.0907	1/33	0.24	0.6290
	Sex	0.0508	1/21	0.76	0.3925	0.0684	1/33	1.92	0.1757
	Distance ^d	-0.0856	1/21	100.99	<0.0001*	0.0106	1/33	0.53	0.4709
7	Whole model		2/21	72.45	<0.0001*		2/33	147.75	<0.0001*
	Constant	1.4090	1/21	261.77	<0.0001*	2.2977	1/33	361.08	<0.0001*
	Sex	-0.1342	1/21	15.41	0.0008*	-0.3818	1/33	141.12	<0.0001*
	Distance ^d	-0.0569	1/21	129.49	<0.0001*	-0.1176	1/33	154.39	<0.0001*
10	Whole model		2/21	14.13	0.0001*		2/33	27.46	<0.0001*
	Constant	1.1755	1/21	49.48	<0.0001*	0.7727	1/33	15.27	0.0004*
	Sex	-0.1733	1/21	6.99	0.0152	-0.3873	1/33	54.30	<0.0001*
	Distance ^d	-0.0442	1/21	21.27	0.0002*	-0.0121	1/33	0.61	0.4406
14	Whole model		2/21	2.49	0.1070		2/33	74.14	<0.0001*
	Constant	0.2314	1/21	7.87	0.0106	2.2571	1/33	207.57	<0.0001*
	Sex	-0.0167	1/21	0.27	0.6120	-0.3594	1/33	74.49	<0.0001*
	Distance ^d	-0.0103	1/21	4.72	0.0415	-0.1053	1/33	73.78	<0.0001*
17	Whole model		2/21	0.14	0.2453		2/33	14.37	<0.0001*
	Constant	0.2760	1/21	0.24	0.0346	1.3994	1/33	45.27	<0.0001*
	Sex	-0.0021	1/21	0.00	0.9657	-0.1969	1/33	12.69	0.0011*
	Distance ^d	-0.0122	1/21	0.14	0.0976	-0.0652	1/33	16.06	0.0003*
21	Whole model		2/21	0.00	1.0000		2/33	4.69	0.0161
	Constant	0.0000	1/21	0.00	1.0000	0.2506	1/33	2.68	0.1113
	Sex	0.0000	1/21	0.00	1.0000	-0.1215	1/33	8.90	0.0053*
	Distance ^d	0.0000	1/21	0.00	1.0000	-0.0083	1/33	0.48	0.4919

The total numbers of adult *S. rubrovittatus* captured on 7 sampling dates until 21 days after the heading date were log-transformed and fitted as multiple responses

^a Numerator/denominator degrees of freedom

^b The *F* value of the whole model is given by approximate *F*-test by Wilks' lambda

^c Level of significance was adjusted by the number of sampling dates; **p* < 0.007

^d Square root of the distance between the bank slope and the sampling point (\sqrt{m})

reported that the immigrations of *S. rubrovittatus* were sometimes observed in the later stage of the grain-filling period in case a very large source habitat surrounded paddies.

Immigration timing may affect the amount and character of the damage to rice. The damage caused by *S. rubrovittatus* differs according to the timing of infestation: infestation during the late grain-filling period caused heavier damage than earlier infestations (Takeda and Shimizu 2009). Although very few comparisons of the population dynamics of *S. rubrovittatus* between paddy fields and source habitats have been reported (Kikuchi et al. 2004),

weeding in the source habitat during the heading period promotes *S. rubrovittatus* immigration into the paddies (Higuchi 2010). Therefore, the timing of weed control should be tested to reduce the damage to rice.

The flight behavior of *S. rubrovittatus* or other Miridae has been reported. The mean flight speed of male *S. rubrovittatus* was measured as 1.20 m/s in the laboratory (Kobayashi 2007). Adult *S. rubrovittatus* flew continuously for at least 3 h (Ando et al., not published). From these dates, the daily potential flight distance of *S. rubrovittatus* can be calculated as about 13 km, much more than the average dispersal distance derived from our estimation.

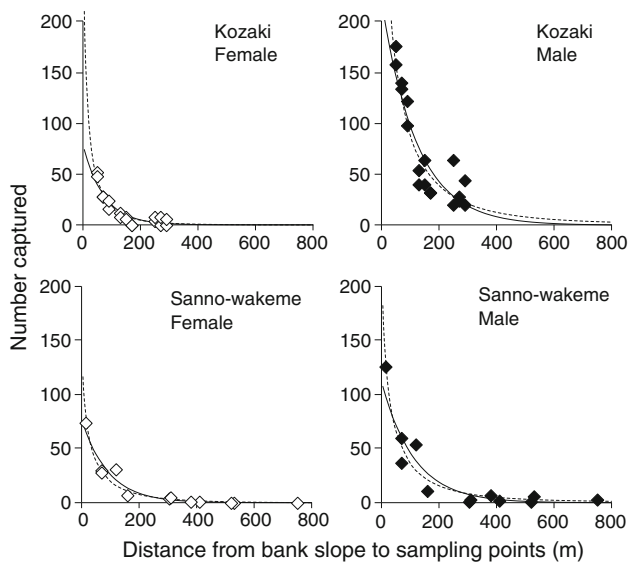


Fig. 5 Relationship between total numbers of adult *Stenotus rubrovittatus* captured and distance from source habitat. *Solid lines*, estimates using the model of Yamamura et al. (2003); *broken lines*, estimates using the model of Wallace (1966). Numbers are totals for invasion period (7–17 days after heading date in Kozaki, 0–10 days after heading date in Sanno-wakeme)

The range of dispersal of insects is usually smaller than the flight distance predicted from a straight line because of undirected flight behavior (Kobayashi 2007). Considering the *S. rubrovittatus* at our study sites flew repeated,

undirected, short flights, the much more limited dispersal area in the field than in the laboratory can be explained.

There have been several reports that arthropod communities were influenced by landscape structures such as the location of surrounding habitats. Yasuda et al. (2011) estimated the functional scale of *S. rubrovittatus* was a radius of 300 m, which reflected the typical dispersal ability and the spatial range of the host plant use. Ichimori et al. (1990) captured a large number of adult *S. rubrovittatus* during the rice heading period at all distances up to 100 m from the source habitat. Ono et al. (2007) reported damage was detected within 100 m from the source habitat. These reports were comparable to our estimate that the average dispersal distance was around 100 m.

Our results also revealed sex differences in flight performance: male *S. rubrovittatus* flew in greater numbers and further than females in both regions. Males flew a bit faster than females in a laboratory experiment (Kobayashi 2007). This difference in flight ability may result in the difference in the average dispersal distance between sexes (Figs. 2, 3). Further laboratory studies will reveal the influence of age and physical condition on flight behavior.

In conclusion, the present study has demonstrated the immigration period and dispersal distance of *S. rubrovittatus* from a large-scale habitat. The immigration period started at the heading date and was prolonged until the late stage of the grain-filling period when the grains of the host

Table 4 Model estimates and *G*-test of deviance ratio

Site	Sex	Model	Parameter	Estimate	SEM	<i>z</i> value	Prob (<i>z</i>)	Deviance (ratio ^a)	Prob (> <i>G</i>)
Kozaki	Female	Wallace (1966) ^b	a	6.06	0.24	25.27	<0.0001***	123.83	
			b	−0.32	0.02	12.82	<0.0001***		
		Yamamura et al. (2003) ^c	c	79.06	10.12	7.81	<0.0001***	138.69	
			d	71.98	6.14	11.72	<0.0001***	(1.12)	>0.05
	Male	Wallace (1966)	a	6.48	0.10	65.47	<0.0001***	203.83	
			b	−0.20	0.01	21.15	<0.0001***		
		Yamamura et al. (2003)	c	220.78	12.13	18.19	<0.0001***	234.87	
			d	121.97	6.15	19.84	<0.0001***	(1.15)	>0.05
Sanno-wakeme	Female	Wallace (1966)	a	5.27	0.15	35.69	<0.0001***	56.53	
			b	−0.23	0.02	13.69	<0.0001***		
		Yamamura et al. (2003)	c	77.42	8.16	9.49	<0.0001***	51.76	
			d	92.05	8.44	10.91	<0.0001***	(1.09)	>0.05
	Male	Wallace (1966)	a	5.67	0.11	50.59	<0.0001***	98.23	
			b	−0.21	0.01	17.47	<0.0001***		
		Yamamura et al. (2003)	c	112.98	8.94	12.64	<0.0001***	121.94	
			d	112.93	7.93	14.24	<0.0001***	(1.24)	>0.05

The response variable was the total number of adult *Stenotus rubrovittatus* captured at 7–17 DAH in Kozaki and at 0–10 DAH in Sanno-wakeme

^a Ratio of higher value to lower value

^b $\log y = a + b\sqrt{x}$ (*x*, distance from bank slope; *y*, abundance of *S. rubrovittatus*; *a* and *b*, constants)

^c $g(y) = c \times \exp(-\frac{x}{d})$

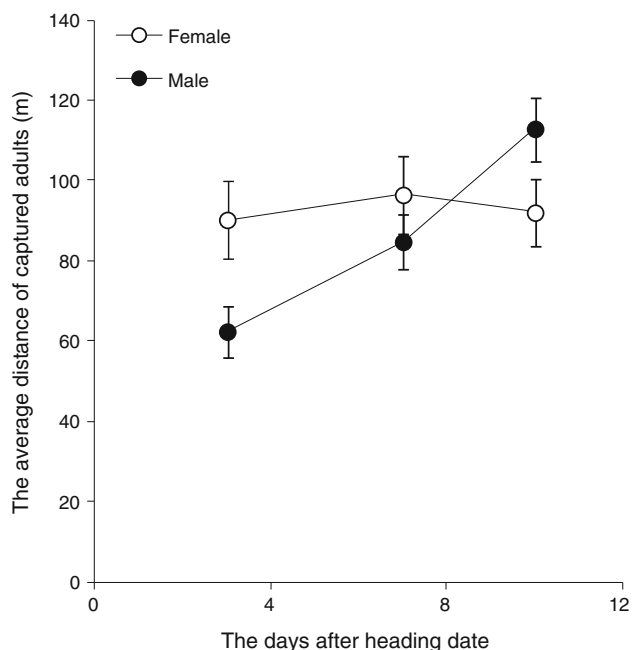


Fig. 6 Average dispersal distances of female and male *Stenotus rubrovittatus* in the early stage of immigration in the Sanno-wakeme region. Bars indicate SEM

plants became suitable food for *S. rubrovittatus*. The average dispersal distance was around 100 m, and the immigration density increased exponentially as the insects approached a large-scale habitat. These facts suggest that gramineous fields need to be kept in improper conditions for *S. rubrovittatus*, which means cutting the weeds from before the beginning of heading of rice plants up to the harvest. In addition, the closer a paddy field is to a large-scale habitat, the more actions need to be taken in areas within a few hundred meters from the large-scale habitat.

Reality is more complicated. Paddy fields are surrounded by many small source habitats such as paddy margins, which influence the occurrence of pecky rice by providing a transit site for the bugs' migration (Yuasa 2006). Not only large- and small-scale source habitats, but also reclaimed land influenced the abundance of *S. rubrovittatus* (Yasuda et al. 2011). Paddy weeds such as *Echinochloa frumentacea* Link or *Scirpus juncooides* Roxb. var. *ohwianus* also attracted *S. rubrovittatus* and increased rice grain damage, because their anthesis is usually earlier than that of rice (Goto et al. 2000; Kashin et al. 2009). These results can be used for the development of strategies to estimate the risk posed by various source habitats.

Habitat manipulation at the landscape level will be increasingly important, because the areas of pastures and abandoned paddies have tended to expand in recent years (Ito 2004; Niiyama 2000). Our knowledge will contribute to the development of strategies to decrease pecky rice

damaged by *S. rubrovittatus* through managing local source habitats where grass weeds are dominant.

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