

**1 Intraspecific variations in life history traits of two pecky rice bug**  
**2 species from Japan: mapping emergence dates and number of annual**  
**3 generations**

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## 20Abstract

21The mirid bugs *Stenotus rubrovittatus* and *Trigonotylus caelestialium*, which cause  
22pecky rice, have become a threat to rice cultivation in Asia. Damage caused by these  
23pests has rapidly become frequent since around 2000 in Japan. Their expansion pattern  
24is not simple, making it difficult to manage them by prediction. Some insects with wide  
25distributions have locally adapted variations in life-history traits. We performed  
26laboratory rearing experiments to assess the geographical scale of intraspecific  
27variations in life-history traits of *S. rubrovittatus* and *T. caelestialium*. These were  
28aimed at increasing the accuracy of occurrence estimates and the number of generations  
29per year. These results were compared with previous research, and differences in  
30development rates were observed between populations of different latitudes, but not of  
31the same latitude. Finally, plotting the timing of adult emergence and the potential  
32number of generations per year on maps with a 5-km grid revealed that they differed  
33greatly locally at the same latitude. These maps can be used for developing more  
34efficient methods of managing mirid bugs in integrated pest management.

35

## 36Key words

37development rate, effective accumulated temperature, geographic variation, local  
38adaptation, risk map.

### 39 Introduction

40 Insects, being poikilotherms, are subjected to strong selection pressure to adapt their life  
41 history traits to habitat temperature (Chown & Terblanche, 2007; Colinet *et al.*, 2015).  
42 Knowledge of the influence of temperature on insects is therefore crucial to understand  
43 changes in seasonal patterns of phenology (Powell & Logan, 2005; Kojima *et al.*, 2020),  
44 distribution (Régnière *et al.*, 2012), and population dynamics (Kingsolver, 1989; Gray,  
45 2008). The relationships between the rate of development of insects and temperature  
46 have been studied in many insect species (Kipyatkov & Lopatina, 2010) to test various  
47 hypotheses of their patterns of adaptation to temperature. Previous studies have focused  
48 mainly on comparison of temperature-dependent development among species or taxa,  
49 and there are few studies of geographical intraspecific variations in development. The  
50 rate of development of less mobile insect species with wide distributions can be  
51 optimized to the local climate (Higaki & Ando, 2002), resulting in geographical  
52 intraspecific variations in the rate of development.

53 Temperature-dependent development of insect pests allows prediction of dates of  
54 emergence, the timing of insecticide applications (Tang & Cheke, 2008), the risk of  
55 outbreaks, and the number of generations per year (Moore & Remais, 2014). Some  
56 studies have used degree-day models that assume a linear relationship between the rate  
57 of development and temperature (Taylor, 1981; Easterbrook *et al.*, 2003) obtained from  
58 limited populations of a species. However, unless the extent of geographic variation in  
59 temperature-dependent development among populations and the spatial scale at which  
60 the variation is determined are known, it remains difficult to explain and predict  
61 population dynamics of a species accurately. Understanding such variations is essential  
62 for establishing effective, locally adapted pest management strategies, such as

63predicting and mapping the timing of dates of emergence and the number of generations  
64per year.

65 Pecky rice bugs are among the most serious economic insect pests of rice (*Oryza*  
66*sativa* L.) in Asia and the USA (Pathak & Khan, 1994; Tindall *et al.*, 2005; Ane &  
67Hussain, 2016). By feeding on rice grains, they leave black spots. Rice showing this  
68type of damage is called pecky rice (Tindall *et al.*, 2005; Kiritani, 2007). In Japan, two  
69mirid bug species—*Stenotus rubrovittatus* (Matsumura) (Hemiptera: Miridae) and  
70*Trigonotylus caelestialium* (Kirkaldy)—have rapidly increased in spread since around  
712000 (Pathak & Khan, 1994; Ohtomo, 2013; Tabuchi *et al.*, 2015). Even a low  
72incidence of pecky rice grains leads to severe economic losses to Japanese farmers  
73under the present national regulation system for rice quality, which depends exclusively  
74on appearance (Watanabe & Higuchi, 2006; Tabuchi *et al.*, 2015). These two mirid bug  
75species are considered to have spread because of global warming (Kiritani, 2007;  
76Osawa *et al.*, 2018b) and an increase in their source habitats such as fallow and meadow  
77fields throughout Japan (Kiritani, 2007; Osawa *et al.*, 2018a). However, higher  
78temperatures and more available habitats cannot systematically explain the difference in  
79expansion patterns among prefectures (Tabuchi *et al.*, 2015), and predicting their future  
80spread remains challenging. A key to untangling the complex expansion pattern of these  
81bugs may be regional adaptation to spatial variations in the thermal environment.

82 Here, we investigated the extent of the geographical variations in life history traits  
83of *S. rubrovittatus* and *T. caelestialium*, whose distribution areas and damage have  
84rapidly expanded throughout Japan in the last two decades. One reason why their  
85distribution expansion pattern differs among prefectures is likely to be population  
86differences in adaptation to temperature. Clarifying the spatial patterns of such

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15geographic variation may reveal the mechanisms of their complex expansion patterns  
16and thus contribute to the establishment of effective, locally adapted pest management  
17strategies in integrated pest management. We compared their life history traits among  
18populations at different spatial scales. We hypothesized that the traits differ between  
19populations widely separated (1) at the same latitude and (2) at different latitudes. To  
20test the first hypothesis, we examined the development times and body size of two  
21geographically separated populations at similar latitudes in the Tohoku region, northern  
22Japan, by rearing them in the laboratory. We examined the rates of development of the  
23egg, nymph, and pre-oviposition stages under five constant rearing temperatures. To test  
24the second hypothesis, we compared the rates of development in the Tohoku region  
25revealed by our experiments and those of previous studies in other areas. We also tested  
26whether the traits differ between sympatric populations of the two species in the Tohoku  
27region. Finally, we mapped the timing of adult emergence of the first generation and the  
28potential number of generations per year, considering the spatial extent of the  
29geographic variation in temperature-dependent development among populations of both  
30species.

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## 32Materials and methods

### 33Study species

34*Stenotus rubrovittatus* and *Trigonotylus caelestialium* are native Japanese mirid bugs  
35widely distributed throughout Japan (Sato & Yasunaga, 1999; Watanabe & Higuchi,  
362006). The adults are ~5 mm in length. The genetic diversity of *S. rubrovittatus* has  
37regional differences, and the species can be roughly divided into three genetic groups in

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110Japan (Kobayashi *et al.*, 2011). Because *S. rubrovittatus* usually feeds on grasses and  
111sedges, it inhabits fallows and meadows around paddy fields (Takada *et al.*, 2012,  
112Shimada and Sugiura 2020), where it reproduces and overwinters (Yoshioka *et al.*,  
1132011). The bugs draw sap from and oviposit in the ears of host plants. The species has a  
114multivoltine life cycle (three or four generations a year; Hayashi & Nakazawa, 1988;  
115Kashin *et al.*, 2009), and overwinters in the egg stage (Hayashi, 1986; Iimura 1992;  
116Goto *et al.*, 2000; Kashin *et al.*, 2009; Nagasawa & Higuchi, 2012). *Trigonotylus*  
117*caelestialium* has similar host plant preferences and a similar life history to *S.*  
118*rubrovittatus* (Okuyama, 1974; Okuyama & Inoue, 1975; Nagasawa & Higuchi, 2012),  
119except for its preference for ovipositioning in the tight gap between the stems and leaves  
120of host plants (Nagasawa *et al.*, 2012). Both species are important pests of cultivated  
121rice, and first- or second-generation adults invade paddy fields and feed on rice ears in  
122August, which is the heading period, causing pecky rice damage (Ono *et al.*, 2007).  
123Crop damage by these species has become a serious problem in the Tohoku region of  
124Japan since around 2000. In the first half of the 2000s, *T. caelestialium* appeared as a  
125major pest species in the prefectures on the Sea of Japan side, including Akita, and *S.*  
126*rubrovittatus* appeared as a major pest species in the prefectures on the Pacific side,  
127including Iwate. Since around 2007, *S. rubrovittatus* became the main pest species also  
128in Akita (Tabuchi *et al.*, 2015).

## 129Development experiments

130We collected *S. rubrovittatus* and *T. caelestialium* in Morioka city, Iwate prefecture  
131(39°45'11.82"N 141°8'9.20"E), in October 2016, and in Akita city, Akita prefecture  
132(39°36'55.3"N 140°11'15.7"E), in June 2017 (Fig. 1). Both species were raised in the  
133laboratory according to the methods of Higuchi and Takahashi (2000) and Nagasawa

134and Higuchi (2010), in transparent acrylamide cages (34 cm × 25 cm × 34 cm, Fujiwara  
135Manufacturing Co., Ltd., Hachioji, Japan). To compare the rates of development  
136between the two populations under experimental conditions where only the temperature  
137was changed, we reared the bugs at 30, 27, 23.5, 20, and 17.5 °C. Eggs were placed in a  
138Petri dish within 24 h after oviposition, and incubated according to Nagasawa and  
139Higuchi (2010). We recorded the number of days from egg collection day to hatching as  
140the ‘egg stage’. We introduced hatched nymphs individually into insect breeding boxes  
141(7.2 cm × 7.2 cm × 10 cm, SPL Life Sciences, Pocheon, Korea). After hatching, we  
142gave six wheat seedlings (1 week after sowing) wrapped in wet cotton to each as food.  
143The food was replaced once every 2 to 6 days, and the number of days from hatching to  
144emergence was recorded as the ‘nymphal stage’. After emergence, only the adult  
145females continued to be reared in the plastic cases, and one male adult of the same  
146population was introduced into each female case for copulation. We provided 6-week-  
147old wheat seedlings as food and 2-day-old seedlings as oviposition substrate. The  
148seedlings were replaced every day, and the presence of eggs was confirmed by  
149dissection of the seedlings. We recorded the number of days from the date of emergence  
150until the day when the first oviposition was confirmed as the ‘pre-oviposition stage’.  
151The rates of development at each temperature were calculated as the reciprocals of the  
152developmental days required for each stage. The lowest development thresholds and the  
153effective accumulated temperatures of each stage were calculated from according to the  
154reduced major axis regression (Ikemoto & Takai, 2001).

155 To test any intraspecific variation in body size between the populations, we  
156measured the thorax width of the adults as an index of body size. We measured females  
157and males reared at 30 and 27 °C, at which many adults were obtained. The widths were

158measured under a stereoscopic microscope with an objective micrometer.

### 159Literature survey

160Data on the average development rates of *S. rubrovittatus* at different temperatures in  
161Shiga and Hiroshima prefectures were obtained from Shigehisa (2004) and Hayashi  
162(1991), respectively. Data on those of *T. caelestialium* at different temperatures in  
163Hokkaido and Niigata prefectures were obtained from Okuyama and Inoue (1975) and  
164Takahashi and Higuchi (2001), respectively.

### 165Statistical analyses

166To test whether the rate of development of each stage differs between the Iwate and  
167Akita populations of each species, we used general linear models (GLMs) with the rate  
168of development as the dependent variable, and temperature, population (Iwate vs.  
169Akita), and their interaction as the predictor variables. Then we compared the rates  
170among the Tohoku (Iwate and Akita) populations and two other prefectures of each  
171species collected previously at different latitudes (Fig. 1) using eight candidate GLMs  
172explaining the rate of development of each stage of each species (Table 1). Model 1  
173assumes that the rate differed among the three populations and was affected by  
174temperature, meaning that these two predictor variables affected the rate independently.  
175Model 2, including the interaction term of the two predictor variables, means that the  
176effect of temperature on the rate differed among the populations. Models 3 and 5 mean  
177that the rate differed between one population and the other two and was affected by  
178temperature. Models 4 and 6, including the interaction term, mean that the effect of  
179temperature on the rate differed between one population and the other two. Model 7  
180means that the rate was affected only by temperature. Model 8, with only the intercept



181term, is the null model. Model selection was performed using Akaike's Information  
182Criteria corrected for small sample size ( $AIC_c$ ; Burnham & Anderson, 2002). A lower  
183 $AIC_c$  value is considered to indicate a better model.  $AIC_c$  was calculated for each model,  
184and models with  $\Delta AIC_c$  (the difference between the  $AIC_c$ s of a focal model and that of  
185the model having the lowest  $AIC_c$ )  $< 2$  were chosen as optimal models. We selected the  
186model with the fewest predictor variables among the optimal models. To test whether  
187the rate of development of each stage differs between the two species in the Tohoku  
188region, we used GLMs with the development rate as the dependent variable, and  
189temperature, species (*S. rubrovittatus* vs. *T. caelestialium*), and their interaction as the  
190predictor variables.

191 To test whether the morphology data differ between the Iwate and Akita  
192populations of each species, we used GLMs with the thorax width as the dependent  
193variable, and sex, population (Iwate vs. Akita), and their interaction as the predictor  
194variables.

195 All analyses were carried out in R v. 3. 3. 1 software (R Development Core Team,  
1962016).

### 197**Estimation of date of theoretical adult emergence and generations per year**

198Using the method of Osawa *et al.* (2018b), we estimated the dates of adult emergence of  
199the first generation and the theoretical annual generation numbers of *S. rubrovittatus*  
200and *T. caelestialium* in Tohoku (Iwate and Akita) in 2013 using the daily mean  
201temperature mesh data of the National Institute for Agro-Environmental Sciences  
202(NIAES) and our data on the two species' development in an effective accumulated  
203temperature (EAT) model. In this study we used temperature data of 2013 for the  
204estimation, because *S. rubrovittatus* was recorded little in the prefectures on the western

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205side in Tohoku region including Akita prefecture around 2000, gradually increased from  
2062003 to 2012, and both two mirid bug species have been recorded throughout the  
207Tohoku region since around 2013 (Tabuchi *et al.*, 2015; Osawa *et al.*, 2018b). We  
208focused on first-generation adults because the emergence day of this generation  
209overlaps the heading stage of rice, when pecky rice damage occurs (Ono *et al.*, 2007).  
210Each 5-km grid cell corresponding to the records of *S. rubrovittatus* and *T.*  
211*caelestialium* occurrence has 25 daily temperature data (Osawa *et al.*, 2018b). EAT of  
212each species was estimated by the triangle method (Sakagami & Korenaga, 1981) with a  
2131 April start date (Murakami *et al.*, 2012; Yokota & Suzuki, 2008). First, we estimated  
214the theoretical egg hatching date using the EAT of the egg stage of each species.  
215Second, we estimated the durations of the nymphal stage of each species from the date  
216when eggs hatched using the EAT of the nymphal stage. Finally, we estimated the  
217sexual maturation date (the end of the pre-oviposition stage) from the date when the  
218nymphal stage ended using the EAT of the pre-oviposition stage. This series of  
219calculations provided an estimate of the generation time for each species' overwintered  
220generation. The first and subsequent generation cycles of each species were estimated  
221using the same procedure from the date of sexual maturation (i.e. start of the oviposition  
222stage) of the proximate generation. Thus, we calculated the span of dates for each  
223development stage and the theoretical generation number in each 1-km grid cell for each  
224species. We ignored the shift from non-diapause to diapause egg production induced by  
225short-day conditions (Okuyama, 1982; Shigehisa, 2008). We also ignored the generation  
226which did not reach the egg-laying stage within a year.

227

## 228Results

## 229 Comparison of development rates at two spatial scales

230 The rate of development at each stage was not significantly different between the Iwate  
 231 and Akita populations of *S. rubrovittatus* (Table 2, Fig. 2a) or *T. caelestialium* (Table 3,  
 232 Fig. 2b). We combined both populations into the ‘Tohoku population’. Model selection  
 233 among the three populations of *S. rubrovittatus* at different latitudes identified model 3  
 234—the rate of development differs between the Hiroshima and the Shiga + Tohoku  
 235 populations—as the best for the egg stage; model 1—it differs among the three  
 236 populations and is affected by temperature—as the best for the nymphal stage; and  
 237 model 7—it is related only to temperature—as the best for the pre-oviposition stage  
 238 (Table 4, Fig. 3a). Model selection among the three populations of *T. caelestialium* at  
 239 different latitudes identified model 3—the rate differs between the Hokkaido and the  
 240 Tohoku + Niigata populations—as the best for the egg stage; and model 4—it differs  
 241 between the Hokkaido and the Tohoku + Niigata populations—as the best for both the  
 242 nymphal and pre-oviposition development stages (Table 4, Fig. 3b).

243     There was no significant difference in the rates of development between species in  
 244 Tohoku at the egg and nymphal stages, but the species  $\times$  temperature interaction was  
 245 significant at the pre-oviposition stage (Table 5, Fig. 4). The developmental zero points  
 246 (i.e., lower developmental threshold) of *S. rubrovittatus* were 12.4 °C in the egg stage,  
 247 10.7 °C in the nymphal stage, and 13.2 °C in the pre-oviposition stage, and those of *T.*  
 248 *caelestialium* were 12.0, 11.9, and 12.7, respectively. The effective accumulated  
 249 temperatures of *S. rubrovittatus* were 102.0 °C-days in the egg stage, 226.3 °C-days in  
 250 the nymphal stage, and 81.8 °C-days in the pre-oviposition stage, and those of *T.*  
 251 *caelestialium* were 95.9, 190.5, and 47.0 °C-days, respectively.

## 252 Body size comparison

We measured the thorax widths of 82 *S. rubrovittatus* and 94 *T. caelestialium* females and males in the 30 and 27 °C treatments. The width of *S. rubrovittatus* was significantly larger in the females than in the males, and in Iwate than in Akita (Table 6, Fig. 5). In *T. caelestialium*, it was also significantly larger in the females, and was significantly larger in Akita than in Iwate (Table 7, Fig. 5).

#### Estimation of date of theoretical adult emergence and generations per year

The date of first emergence of *S. rubrovittatus* adults in 2013 was estimated to be 29 July, and the median was 19 August (Fig. 6a). Those of *T. caelestialium* were 22 July and 11 August, respectively (Fig. 6b). In *S. rubrovittatus*, 84.5% of the 5-km grid cells in Iwate and Akita showed successful completion of the second generation, and 27.2% of the cells (some inland cells in Iwate and some coastal cells in Akita) showed successful completion of the third generation (Fig. 7a). In *T. caelestialium*, 54.5% of the cells showed successful completion of the third generation, and 2.7% showed successful completion of the fourth generation (Fig. 7b).

#### Discussion

There was no difference in the relationship between temperature and the rate of development in each developmental stage of the two mirid bug species from the same latitude in northern Japan. On the other hand, the relationship showed geographical variations between populations of both species at different latitudes.

The rates of development of the two species were higher in the southern populations (Fig. 3). That of *S. rubrovittatus* was higher in Hiroshima, the southernmost of the three populations, and that of *T. caelestialium* was lower in Hokkaido, the northernmost population. The adaptive significance of the geographic intraspecific

variation in development rates has not been adequately validated in many insect species (Kipyatkov & Lopatina, 2010). Higher development rates in low-latitude populations may increase the number of generations. In this analysis, it cannot be ignored that the diets used in the rearing experiments differed among our and the previous studies (Hayashi, 1991; Shigehisa 2004; Okuyama & Inoue, 1975). The response of insect development to temperature depends on diet (Goryshin *et al.*, 1988; Ayres & Scriber, 1994). The Hiroshima population of *S. rubrovittatus* in Hayashi (1991) was reared on ears of *Lolium multiflorum*, one of the plants most preferred by the bug (Nagasawa & Higuchi, 2012), and this may have caused the high development rate. The Hokkaido population of *T. caelestialium* in Okuyama and Inoue (1975) was reared on rice leaves, which are less preferred than some grass and sedge weeds, and this may have caused the low development rate. Nevertheless, the two mirid bug species are likely to have variations in rates of development between latitudes, because differences in the response to temperature were found among the populations even at the egg stage, when the influence of diet can be ignored (Fig. 3). In any case, we revealed that the difference in development rates of the two species was not observed between populations of the same latitude in the Tohoku region by our rearing experiments. In addition, we also showed that there was no difference in the relationship between temperature and the rate of development of *T. caelestialium* between populations of Tohoku region and Niigata prefecture (Fig. 1), because the diet of the bug used in our rearing experiments was the same as that in Takahashi and Higuchi (2001) having data on the development rates of the bug in Niigata prefecture. To clarify the extent of geographic variation in temperature-dependent development among populations of the two mirid bugs more clearly, it is necessary to conduct similar rearing experiments with many populations

301from more diverse latitudes.

302     The adult body size of both sexes of *S. rubrovittatus* was larger in Iwate and that of  
303*T. caelestialium* was larger in Akita (Tables 6, 7, Fig. 5), but there was no difference in  
304the rates of development of each stage between the Iwate and Akita populations. We  
305consider the two populations of the two species to be independent, as variations in body  
306size were observed in those reared under the same experimental conditions. One reason  
307for their independence despite the short distance of about 85 km between the collection  
308sites is the presence of the Ou Mountains, with peaks of up to 2000 m in elevation  
309between the prefectures. Population dynamics may differ between the two populations  
310in both species, as it is known that female fertility and survival rate in insects increase  
311with body size (Honěk, 1993; Lighton *et al.*, 1994; Parker & Simmons, 1994;  
312Blanckenhorn, 2000; Rivero & West, 2002). The body size also differed between the  
313sexes: the females were significantly larger in both species (Tables 6, 7, Fig. 5), but the  
314population  $\times$  sex interaction was not significant in either species (Tables 6, 7). These  
315results are consistent with the report that female *T. caelestialium* have longer forewing  
316length (Higuchi & Takahashi, 2000; Nagasawa & Higuchi, 2012). The generally larger  
317size of female insects (Fairbairn, 1997; Blanckenhorn *et al.*, 2007) is thought to be  
318associated with female reproductive traits (Fairbairn, 2005). Although we cannot  
319identify the adaptive significance of the large female size from our results, it may affect  
320the reproductive success of the two mirid bug species.

321     We mapped the timing of adult emergence of the first generation and the potential  
322number of generations per year only within Iwate and Akita prefectures using the daily  
323mean temperature in 2013 and our data on the two species' development in an EAT  
324model, because our results showed no difference in the temperature dependence of

development between populations at the same latitude, but showed geographic variation among populations at different latitudes. The estimation of adult emergence date of the first generation showed about 8 days' difference between species in both the first day and the median day. Thus, *T. caelestialium* adults emerged a week earlier than *S. rubrovittatus* (Fig. 6). In both Iwate and Akita prefectures, the adult emergence dates differed locally even at the same latitude (Fig. 6). These results suggest that the timing at which adults first emerge in Iwate and Akita and move to the paddy fields differs greatly both between and within species. The estimates suggest that *T. caelestialium* can successfully reproduce four generations per year, one generation more than *S. rubrovittatus* in some areas (Fig. 7). In Akita, *T. caelestialium* was the main species in the early 2000s (Tabuchi *et al.*, 2015). Its estimated ability to reproduce one more generation may be related to its rapid increase to major pest status in Akita. Simultaneous mowing of fallow fields and footpaths, the bugs' main habitats, is recommended for the control of the flightless nymphal stages (Watanabe & Higuchi, 2006). The large differences among the estimated dates of adult emergence both within and between species at the 5-km scale suggest that the optimum timing of such management also differs locally.

Although there was no difference in the rates of development between populations at the same latitude, the results support our hypothesis that the relationship between temperature and rate of development differs between populations at different latitudes, being higher in the southern populations. However, the extent of the difference depends on species and development stage. These results suggest that differences in the relationship between temperature and rate of development among insect populations are not determined at a specific developmental stage, and investigating only specific stages

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349may reduce the accuracy of results. Therefore, it is important to investigate  
350developmental days and rates of development throughout the entire life cycle. Our  
351estimates of the dates of adult emergence and the numbers of annual generations  
352revealed that the timing of emergence differs between the two mirid bug species by  
353about a week, and differs greatly even within a species locally at the same latitude. By  
354combining the rates of development of each species between sites in Tohoku with  
355climate change forecasts, it may be possible to predict when and where the first  
356generation adults of each species will invade paddy fields each year in the future. This  
357technique could be used for developing more efficient methods of managing pecky rice  
358bugs in integrated pest management.

359

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### 367**Conflict of interest**

368The authors declare that they have no conflict of interest.

369

### 370**Data accessibility**

371The data that support the findings of this study will be archived in the Dryad system



372upon acceptance.

### 374**Author contributions**

375KY, KT, OT, AY, and MBT designed the experiments. AT, YI, and SS provided  
376technical and material support. KY, KT, AT, and OT collected the samples. KY, KT,  
377OT, AY, and MBT performed the experiments, analyzed the data and wrote the  
378manuscript. All authors read and approved the manuscript.

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555**Tables**

556**Table 1** Models of the development rates of *Stenotus rubrovittatus* and *Trigonotylus*  
 557*caelestialium* in three latitudinally different populations of each species

No.	Models
<i>S. rubrovittatus</i>	
1	Three populations + temperature
2	Three populations + temperature + three populations * temperature
3	Populations (Tohoku-Shiga vs Hiroshima) + temperature
4	Populations (Tohoku-Shiga vs Hiroshima) + temperature + populations (Tohoku-Shiga vs Hiroshima) * temperature
5	Populations (Tohoku vs Shiga-Hiroshima) + temperature
6	Populations (Tohoku vs Shiga-Hiroshima) + temperature + populations (Tohoku vs Shiga-Hiroshima) * temperature
7	Temperature
8	Intercept
<i>T. caelestialium</i>	
1	Three populations + temperature
2	Three populations + temperature + three populations * temperature
3	Populations (Hokkaido vs Touhoku-Niigata) + temperature
4	Populations (Hokkaido vs Tohoku-Niigata) + temperature + populations (Hokkaido vs Tohoku-Niigata) * temperature
5	Populations (Niigata vs Tohoku-Hokkaido) + temperature
6	Populations (Niigata vs Tohoku-Hokkaido) + temperature + populations (Niigata vs Tohoku-Hokkaido) * temperature
7	Temperature
8	Intercept

559**Table 2** Effects of each parameter on the development rates of *Stenotus rubrovittatus* in  
 560Iwate and Akita

Stage	Parameter	<i>Df</i>	Sum Sq	<i>F</i>	<i>Pr(&gt;F)</i>
Egg	Temperature	1	0.0189	366.0408	<0.001
	Population	1	0.0000	0.0023	0.9632
	Temperature×Population	1	0.0000	0.0057	0.9424
	Residuals	6	0.0003		
Nymph	Temperature	1	0.0039	177.7902	<0.001
	Population	1	0.0000	0.2982	0.6047
	Temperature×Population	1	0.0000	0.2278	0.6500
	Residuals	6	0.0001		
Pre- oviposition	Temperature	1	0.0201	77.8685	<0.001
	Population	1	0.0000	0.0029	0.9595
	Temperature×Population	1	0.0000	0.0020	0.9660
	Residuals	5	0.0013		

561

**Table 3** Effects of each parameter on the development rates of *Trigonotylus caelestialium* in Iwate and Akita

Stage	Parameter	<i>Df</i>	Sum Sq	<i>F</i>	<i>Pr(&gt;F)</i>
Egg	Temperature	1	0.0234	397.0632	<0.001
	Population	1	0.0000	0.2268	0.6508
	Temperature×Population	1	0.0000	0.1943	0.6748
	Residuals	6	0.0004		
Nymph	Temperature	1	0.0060	246.3485	<0.001
	Population	1	0.0000	0.1295	0.7313
	Temperature×Population	1	0.0000	0.1102	0.7512
	Residuals	6	0.0001		
Pre-oviposition	Temperature	1	0.0547	262.1049	<0.001
	Population	1	0.0000	0.2352	0.6482
	Temperature×Population	1	0.0000	0.1209	0.7423
	Residuals	5	0.0010		

**Table 4** Eight candidate models explaining the development rate in each stage of *Stenotus rubrovittatus* and *Trigonotylus caelestialium* and their information-theoretic statistics

Mode l	Variables included in the model			Egg		Nymph		Pre-oviposition <sup>†</sup>	
				AICc	ΔAICc ‡	AICc	ΔAICc ‡	AICc	ΔAICc ‡
<i>S. rubrovittatus</i>									
1	Temperature	Population (Tohoku, Shiga, vs. Hiroshima)	Their interaction	-	-	-	-	-	-
				106.5	5.47	109.9	0.00	-42.5	1.76
2	Temperature	Population (Tohoku, Shiga, vs. Hiroshima)		-99.9	11.99	107.2	2.70	-42.3	1.96
3	Temperature	Population (Tohoku vs. the other two populations)	Their interaction	-	-	-	-	-	-
				110.8	1.16	105.8	4.05	-	-
4	Temperature	Population (Tohoku vs. the other two populations)		-	0.00	103.2	6.71	-	-
5	Temperature	Population (Hiroshima vs. the other two populations)	Their interaction	-	-	-	-	-	-
				-99.5	12.38	104.5	5.33	-	-
6	Temperature	Population (Hiroshima vs. the other two populations)		-95.8	16.17	104.1	5.78	-	-
7	Temperature			-	-	-	-	-	-
				100.9	11.04	-96.1	13.81	44.29	0.00
8	Intercept only			-50.3	61.58	-65.7	44.21	22.32	21.96
				Egg		Nymph		Pre-oviposition	
				AICc	ΔAICc ‡	AICc	ΔAICc ‡	AICc	ΔAICc ‡
<i>T. caelestialium</i>									
1	Temperature	Population (Hokkaido, Tohoku, vs. Niigata)	Their interaction	-	-	-	-	-	-
				79.66	2.98	74.36	21.83	42.02	28.06
2	Temperature	Population (Hokkaido, Tohoku, vs. Niigata)		74.78	7.86	81.58	14.62	62.46	7.63
3	Temperature	Population (Hokkaido, vs. the other two populations)	Their interaction	-	-	-	-	-	-
				81.38	1.26	79.51	16.69	46.65	23.44
4	Temperature	Population (Hokkaido, vs. the other two populations)		-	0.00	96.19	0.00	70.09	0.00
5	Temperature	Population (Niigata, vs. the other two populations)	Their interaction	-	-	-	-	-	-
				80.43	2.21	77.53	18.66	37.67	32.41
6	Temperature	Population (Niigata, vs. the other two populations)		75.82	6.82	76.14	20.05	33.77	36.31
7	Temperature			-	-	-	-	-	-
				77.80	4.84	80.12	16.07	38.99	31.09
8	Intercept only			37.78	120.42	52.99	43.20	21.29	48.80

<sup>†</sup>No data was available from Hayashi (1991).

<sup>‡</sup> $\Delta$ AICc is the difference between the AICcs of a focal model and that of the model having the lowest AICc.

573**Table 5** Effects of each parameter on the development rates of *Stenotus rubrovittatus*  
 574and *Trigonotylus caelestialium* in Tohoku

Stage	Parameter	<i>Df</i>	Sum Sq	<i>F</i>	<i>Pr(&gt;F)</i>
Egg	Species	1	0.0000	0.4471	0.5286
	Temperature	1	0.0118	222.2840	<0.001
	Species×Temperature	1	0.0001	1.3827	0.2842
	Residuals	6	0.0003		
Nymph	Species	1	0.0000	2.3140	0.1790
	Temperature	1	0.0032	215.5026	<0.001
	Species×Temperature	1	0.0001	3.7696	0.1002
	Residuals	6	0.0001		
Preoviposition	Species	1	0.0009	5.7406	0.0536
	Temperature	1	0.0418	281.3929	<0.001
	Species×Temperature	1	0.0038	25.3141	0.0024
	Residuals	6	0.0009		

576**Table 6** Effects of each parameter on the thorax width of *Stenotus rubrovittatus*

Parameter	<i>Df</i>	Sum Sq	<i>F</i>	<i>Pr(&gt;F)</i>
Population	1	0.0210	4.9147	0.0294
Sex	1	0.3270	76.1879	<0.001
Population×Gender	1	0.0020	0.4416	0.5082
Residuals	81	0.3480		

578**Table 7** Effects of each parameter on the thorax width of *Trigonotylus caelestialium*

Parameter	<i>Df</i>	Sum Sq	<i>F</i>	<i>Pr(&gt;F)</i>
Population	1	0.0170	4.4743	0.0371
Sex	1	0.2000	52.3055	<0.001
Population×Gender	1	0.0090	2.2384	0.1380
Residuals	93	0.3550		

## 580Figure Legends

581**Figure 1** Sites where *Trigonotylus caelestialium* and *Stenotus rubrovittatus* were  
 582collected.  $\Delta$  Both species collected by us in (1) Iwate Prefecture in 2016 and (2) Akita  
 583prefecture in 2017.  $\circ$  *T. caelestialium* collected by (1) Okuyama and Inoue (1975) and  
 584(2) Takahashi and Higuchi (2001).  $\square$  *S. rubrovittatus* collected by (1) Hayashi (1991)  
 585and (2) Shigehisa (2004). Coastlines and boundaries were obtained from the Database  
 586of Global Administrative Areas (<https://gadm.org/>).

587**Figure 2** Relationships between temperature and development rate of (a) *Stenotus*  
 588*rubrovittatus* and (b) *Trigonotylus caelestialium* in Iwate ( $\circ$ ) and Akita ( $\square$ ) populations  
 589at each developmental stage.

590**Figure 3** Relationships between temperature and development rate of (a) *Stenotus*  
 591*rubrovittatus* in Tohoku region ( $\bullet$ ), Shiga ( $\Delta$ ), and Hiroshima ( $\square$ ) prefectures and (b)  
 592*Trigonotylus caelestialium* in Tohoku region ( $\circ$ ), Niigata ( $\blacktriangle$ ), and Hokkaido ( $\blacksquare$ )  
 593prefectures at each developmental stage. Each line indicates the relationship between  
 594temperature and development rate in each population.

595**Figure 4** Relationships between temperature and development rate of *Stenotus*  
 596*rubrovittatus* ( $\circ$ ) and *Trigonotylus caelestialium* ( $\square$ ) in Tohoku populations.

597**Figure 5** Thorax width (mean  $\pm$  SE) of male ( $\square$ ) and female ( $\blacksquare$ ) (a) *Stenotus*  
 598*rubrovittatus* and (b) *Trigonotylus caelestialium* in Iwate and Akita populations.

599**Figure 6** Average theoretical emergence dates of first generation of (a) *Stenotus*  
 600*rubrovittatus* and (b) *Trigonotylus caelestialium* based on effective accumulated  
 601temperature in 2013.

602**Figure 7** Average theoretical generation numbers of (a) *Stenotus rubrovittatus* and (b)  
 603*Trigonotylus caelestialium* based on effective accumulated temperature in 2013.