



# Robustness of latitudinal life-cycle variations in a cricket *Dianemobius nigrofasciatus* (Orthoptera: Trigonidiidae) in Japan against climate warming over the last five decades

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## Abstract

Recent climate warming is expected to have changed the phenology of organisms. The cricket *Dianemobius nigrofasciatus* (Matsumura) (Orthoptera: Trigonidiidae) has univoltine and bivoltine life cycles in northern and southern regions of Japan, respectively, because of latitudinal variation in the growing season length. Its adult body size increases with decreasing latitude, and decreases at a latitude where the number of annual generations increases. The present study aims to examine whether the range of the bivoltine life cycle has expanded northward due to climate warming. We compared a latitudinal saw-tooth body size cline between the 1960s and the 2010s. The body size showed a latitudinal saw-tooth cline in adults collected in recent years, as it did in adults collected five decades ago. However, no significant difference was observed between these two clines, suggesting that the bivoltine life cycle has not expanded in the last five decades. These results contrast to those recently reported in a closely related species, *Polionemobius mikado* (Shiraki) (Orthoptera: Trigonidiidae), in which the turning points of the saw-tooth cline had shifted northward in the last four decades. The stable latitudinal distribution of life cycles in *D. nigrofasciatus* might result from the different photoperiodic regulation of growth rate involved in the different responses to climate warming.

**Keywords** Body size · Geographic variation · Latitude · Saw-tooth cline · Season length

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## Introduction

Climate warming affects ecological characteristics of organisms, including phenology and body size (Parmesan and Yohe 2003; Scheffers et al. 2016; Walther et al. 2002). In insects with short generation time, the number of annual generations (voltinism) is predicted to increase with increasing length of the season available for growth (Forrest 2016; Yamamura and Kiritani 1998), and some field observations indicate that it has increased in several decades as expected (Altermatt 2010; Martín-Vertedor et al. 2010; Mitton and Ferrenberg 2012). Moreover, the growing season length declines with increasing latitude, and a species with a wide distribution often shows a latitudinal variation in voltinism (Tauber et al. 1986). In this case, mathematical models predict that climate warming will relax the constraint of the growing season length, and the typical life cycle at lower latitudes will expand into higher latitudes by the end of the 21st century (Braune et al. 2008; Jönsson et al. 2009). However, it is also considered likely that increasing temperature

sometimes causes unexpected maladaptive consequences for insect populations (Grevstad and Coop 2015; Musolin 2007; Van Dyck et al. 2015). Thus, the phenological changes that have actually occurred in recent decades need to be investigated to precisely predict the future responses to climate warming.

In addition to voltinism, insect body size also shows several types of latitudinal clines, including both positive and negative correlations (Blanckenhorn and Demont 2004; Mousseau 1997; Shelomi 2012). Generally, a higher rearing temperature results in a smaller adult body size in ectotherms (Atkinson 1994; Van Voorhies 1996). This “temperature–size rule” is thought to be involved in the positive relationship between body size and latitude in *Drosophila* spp. (David and Bocquet 1975; James et al. 1997; Partridge and French 1996), and also in a decreasing body size in relation to climate warming in several other species of insects (Blanckenhorn 2015; Bowden et al. 2015; Tseng et al. 2018), fishes (Baudron et al. 2014; Daufresne et al. 2009), amphibians (Caruso et al. 2015; Reading 2007; Sheridan et al. 2018), and reptiles (López-Calderón et al. 2017). In a univoltine insect, however, the constraint of the growing season length is more important than the negative effect of higher temperature on body size, and therefore body size often decreases with increasing latitude (Masaki 1967; Nylin and Svärd 1991; Park 1949). Moreover, in a species that shows a latitudinal change of its life cycle from bivoltine to univoltine, body size sometimes shows a “saw-tooth” latitudinal cline: Body size decreases with increasing latitude, and increases sharply at the latitude where the length of the growing season becomes insufficient for the bivoltine life cycle to be completed. Masaki (1972) first demonstrated this latitudinal saw-tooth model in the band-legged ground cricket, *Dianemobius nigrofasciatus* (Matsumura) (Orthoptera: Trigonidiidae), formerly known as *Pteronemobius fascipes* Walker (Masaki 1983). This species has univoltine and bivoltine life cycles in the northern and southern regions of Japan, respectively, and overwinters as diapause eggs. Masaki (1972) collected adults of *D. nigrofasciatus* over a wide range of latitudes from 1965 to 1970, and found that their body size showed a latitudinal saw-tooth cline related to the latitudinal variation in voltinism: The body size decreased north to approximately 37°N, then sharply increased to approximately 39°N and again decreased to approximately 44°N. In the middle segment of the cline where the body size increased with increasing latitude, univoltine and bivoltine life cycles were intermingled (Kidokoro and Masaki 1978; Masaki 1972, 1978a). Since then, saw-tooth relationships between body size and latitude (or growing season length) have been reported in several insect species (Johansson 2003; Masaki 1978b; Mousseau and Roff 1989; Nylin and Svärd, 1991). Applying

the latitudinal saw-tooth model in the context of climate warming, the latitudinal expansion of the bivoltine life cycle would be predicted to be accompanied by a latitudinal shift in the turning points of the saw-tooth cline. Even if a saw-tooth body size cline had not shifted latitudinally, one could examine whether the body size was affected directly by increasing temperature due to climate warming. Recently, it was shown that the lower and upper turning points of the saw-tooth body size cline had shifted northward by 1–2° (100–200 km in distance) from the 1970s to the 2010s in relation to an increase in the growing season length in the lawn ground cricket, *Polionemobius mikado* (Shiraki) (Matsuda et al. 2018). Thus, comparing the past and more recent saw-tooth clines is recognized as a method that saves time and effort to evaluate the temporal change in insect voltinism and body size over a wide range of latitudes. Although *D. nigrofasciatus* and *P. mikado* have similar life cycles, they have different photoperiodic regulation of the nymphal development time underlying their different phenology (see Fig. 5a; Masaki 1972, 1979). There are substantial latitudinal variations in the nymphal development time and its photoperiodic variability, affecting the latitudinal patterns in voltinism in the two species. Notably, the nymphal development time of *D. nigrofasciatus* originating from bivoltine populations becomes longer under intermediate daylengths; whereas, the nymphal development time of *D. nigrofasciatus* originating from univoltine ones and of *P. mikado* become longer under long days. Therefore, adults of the overwintering generation of *D. nigrofasciatus* emerge earlier than those of *P. mikado* due to long days in summer delaying the nymphal development of *P. mikado* (Masaki 1979). In autumn, however, adults of the two species emerge in the same period of the year due to intermediate daylengths delaying the nymphal development of *D. nigrofasciatus* (Masaki 1972). In this respect, *D. nigrofasciatus* is a suitable subject for examining whether insects show a common life-history response to climate warming. The report by Masaki (1972) provides not only the past data on body size of *D. nigrofasciatus* necessary for comparison with the more recent ones, but also useful information on other life-history traits involved in voltinism.

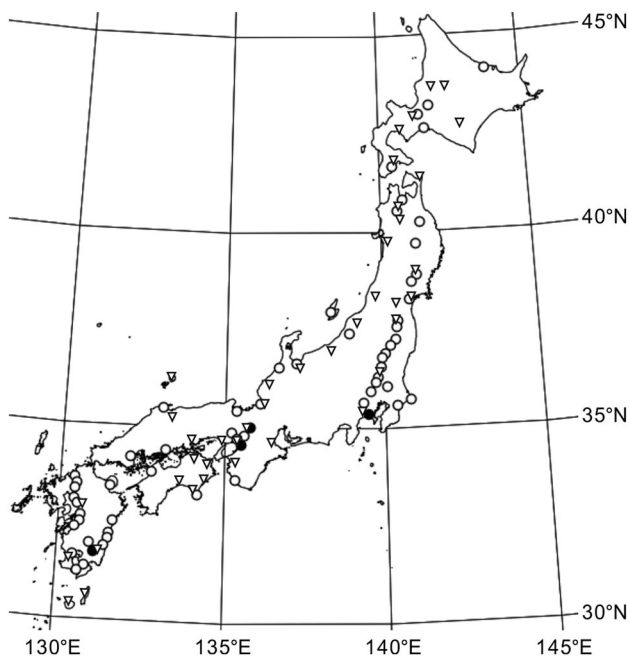
The present study aims to examine the temporal change in the latitudinal variation of voltinism of *D. nigrofasciatus*. First, we examined whether the body size of adult *D. nigrofasciatus* collected in the 2010s showed a latitudinal saw-tooth cline, as did the body size of adults in the 1960s (Masaki 1972). Second, we examined whether the latitudinal distribution of univoltine and bivoltine life cycles had changed during the last five decades by comparing the latitudinal body size cline between the 1960s and 2010s. Third, we compared the sum of effective temperatures for development of *D. nigrofasciatus* between the 1960s

and 2010s as an index of the growing season length, and showed that climate warming could potentially affect the latitudinal variation in the voltinism of *D. nigrofasciatus*.

## Materials and methods

### Insects

Adults of *D. nigrofasciatus* were collected from 62 sites in Japan from August to October in 2015–2018 (see Fig. 1 and Online Resource: Table S1). A total of 6566 adults were collected, and the mean number per site was 48 and 40 for females and males, respectively. The sampling sites extended from the southernmost site in Ibusuki City (31.2°N, 130.6°E) to the northernmost site in Saroma Town (44.1°N, 143.8°E). In general, the sampling dates were earlier at higher latitudes, because of a latitudinal difference in the period of adult emergence. Altitudes of these sites were lower than 363 m above sea level to exclude variations in body size due to altitude. Adults were preserved in 70% ethanol for measurement of the body size.



**Fig. 1** Sampling localities of adult *Dianemobius nigrofasciatus*. Open and closed circles show localities in which adults were collected in a single year of 2015–2018 and in all of the 4 years, respectively. Triangles show localities in which adults were collected in 1965–1970 by Masaki (1972)

### Measurement of body size

The width of the head, including the compound eyes, was measured as an index of the body size, using a stereomicroscope (S8 APO; Leica Microsystems, Wetzlar, Germany) and ScopeImage 9.0 imaging software (Nanjing Jiangnan Novel Optics Co., Ltd., Nanjing, China), because this width is closely correlated with other dimensions of sclerotized parts of the body (Masaki 1972). The coefficient of variation (C.V.) of the head width was also calculated because it was expected to become larger at latitudes at which the univoltine and bivoltine life cycles were intermingled.

Data of the head width of adults collected in autumn in 1965–1970 were derived from Masaki (1972). He collected a total of approximately 2000 female and 1400 male adults from 40 sites between 30 and 44°N in Japan (Fig. 1). Altitudes of these sampling sites were lower than 150 m above sea level. The mean head width for every degree of latitude was calculated for both sexes.

### Estimation of the sum of effective temperatures

To quantify the temporal change in the growing season length of *D. nigrofasciatus*, the sum of effective temperatures for development from spring to autumn was compared between means in 1965–1970 and 2015–2018 at seven sites, Miyakonojo (31.7°N, 131.1°E), Fukuoka (33.6°N, 130.4°E), Osaka (34.6°N, 135.5°E), Utsunomiya (36.6°N, 139.9°E), Sendai (38.3°N, 140.9°E), Morioka (39.7°N, 141.1°E) and Sapporo (43.0°N, 141.4°E). These sites were chosen from the sampling sites of *D. nigrofasciatus* in 2015–2018. The end of the growing season was defined as the first day after which the daily mean temperature fell below the lower development threshold for more than two successive days. Assuming that the lower threshold of development was 10 °C (Masaki 1972), the sum of effective temperatures above 10 °C at each site was calculated. Records of daily mean temperature were retrieved from a database on the website of the Japan Meteorological Agency (2019).

### Statistical analyses

Analyses were carried out using R 3.5.2 (R Core Team 2018). Samples collected in 2015–2018 were pooled after it was determined whether the head width differs significantly among these four sampling years. This was tested using adult *D. nigrofasciatus* collected at four sites, namely Miyakonojo (31.7°N, 131.1°E), Osaka (34.6°N, 135.5°E), Kyoto (35.0°N, 135.8°E), and Fujisawa (35.4°N, 139.5°E), at which adults were collected during the 4 years (Fig. 1). A three-way analysis of variance was applied to test the effect of sex, the sampling site and the sampling year on the head width of adults collected from the four sites. A

generalized additive model was applied to fit a spline curve to the relationship between the head width and the latitude of the sampling site, and test the effect of sex, latitude, year (2015–2018) and period (1965–1970 and 2015–2018) on the head width, using *R* package *mgcv*. For convenience, the latitudes of the sampling sites in 1965–1970 were shown as the center of every degree; i.e., 30.5, 31.5, 32.5, ..., 43.5°N, as in Masaki (1972).

## Results

### Body size in 2015–2018

A three-way analysis of variance showed that sex, the sampling site and the sampling year had significant effects on the head width of adult *D. nigrofasciatus* collected from the four sites with a wide range of latitudes in 2015–2018 (Fig. 2, Table 1). Therefore, the sampling year was used as an explanatory variable for further analyses. There was a latitudinal variation in the head width of adults collected in 2015–2018 in both sexes (Fig. 3). The fitted spline curve showed a latitudinal saw-tooth relationship between the head width and the latitude of the sampling site: the head width was approximately constant at latitudes from 31°N to 37°N, it increased as latitude increased to 40°N, and then it decreased when latitude further increased to 44°N. Within each site, the head width was larger in both females than in males. The coefficient of variation (C.V.) of the head width increased as latitude increased to around 36°N or 37°N, and then decreased to 44°N, in females and males, respectively

**Table 1** A three-way analysis of variance to test the effect of variables on the head width of adult *Dianemobius nigrofasciatus* in 2015–2018

Variable	<i>df</i>	MS	<i>F</i> value	<i>P</i> value
Sex (A)	1	6.35	1320.7	<0.001
Site (B)	3	0.209	43.521	<0.001
Year (C)	3	0.0827	17.190	<0.001
A × B	3	0.0191	3.9711	0.00783
A × C	3	0.0038	0.7956	0.496
B × C	9	0.0572	11.898	<0.001
A × B × C	9	0.0265	0.6122	0.788
Residuals	1615	7.7686	0.0048	

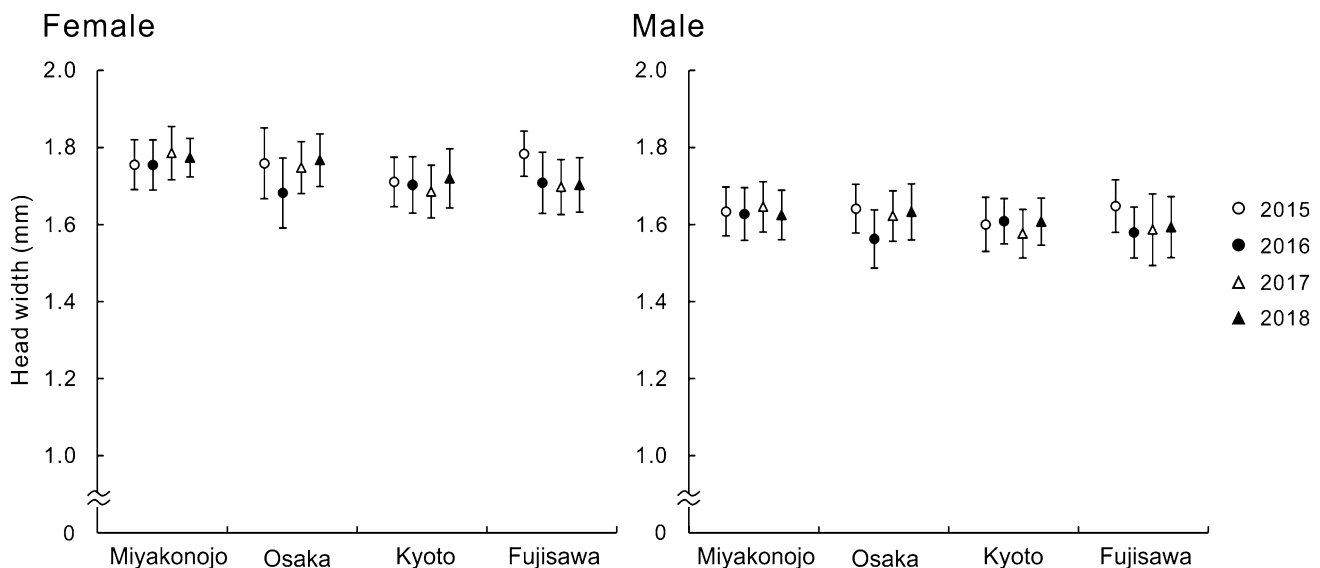
Adults were collected from four sites at different latitudes in all the 4 years

*df* degrees of freedom, *MS* mean square

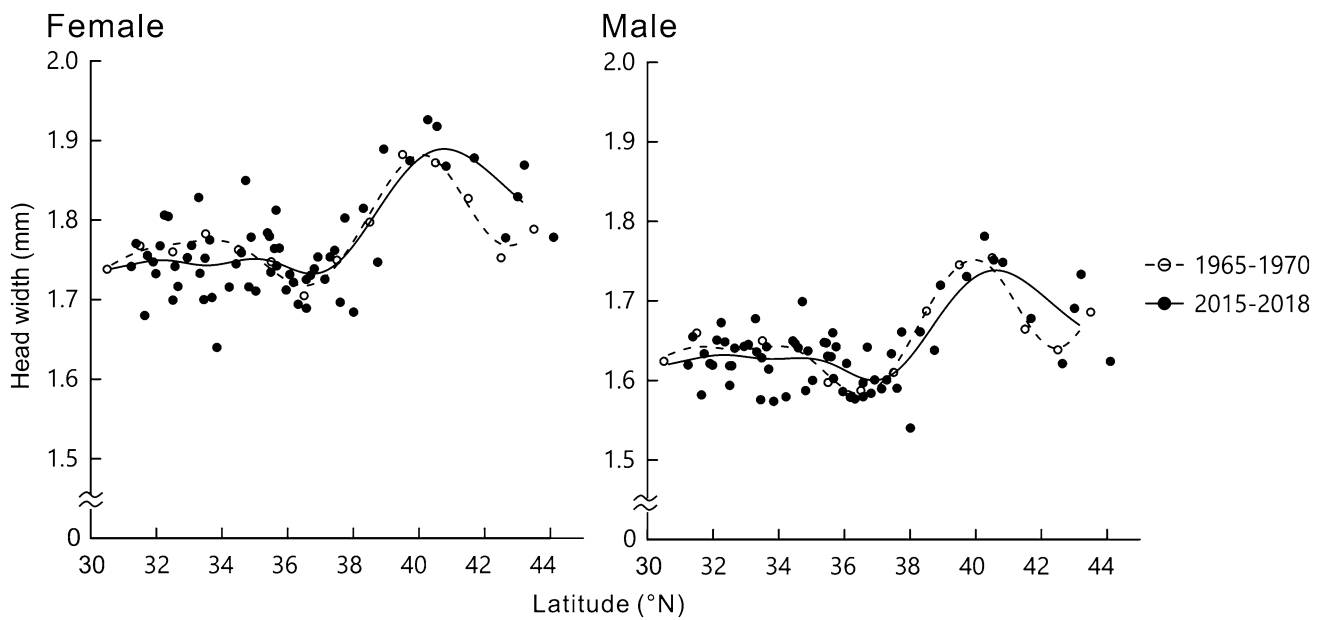
(see Online Resource: Fig. S1). However, adult *D. nigrofasciatus* collected at Matsuyama City (33.8°N, 132.8°E) on September 3, 2017 showed an exceptionally large C.V. of the head width compared to that at the other sites, possibly because the sampling date was earlier than those at the other sites at the same range of latitudes (from late September to early October). Therefore, the samples obtained in Matsuyama City were excluded from further analyses.

### Comparison of body size between 1965–1970 and 2015–2018

There was little or no difference in the saw-tooth body size cline between adult *D. nigrofasciatus* collected in



**Fig. 2** Comparisons of adult head widths of *Dianemobius nigrofasciatus* within four collection sites, Miyakonojo (31.7°N), Osaka (34.6°N), Kyoto (35.0°N) and Fujisawa (35.4°N), among sampling years of 2015–2018 (females,  $n=25$ –130; males,  $n=23$ –77, mean  $\pm$  SD)



**Fig. 3** Mean head width of adult *Dianemobius nigrofasciatus* in relation to latitude. Adults were collected in autumn in 1965–1970 [based on the data of Masaki (1972),  $n=20-600$ ] and in 2015–2018 (females,  $n=20-98$ ; males,  $n=13-91$ ). The spline curves are fit-

ted to the relationship between the head width and the latitude of the site. Note that the mean head width was plotted for every degree of latitude in 1965–1970, whereas the mean head width was plotted for every site in 2015–2018

1965–1970 and 2015–2018 (Fig. 3). Over this time span (about five decades), the upper and lower turning points of the cline had shifted northward by less than 1° in both sexes. A generalized additive model showed that sex and the latitude of the sampling site had significant effects on the head width, whereas neither the sampling year, period nor the interactions of any of these variables had a significant effect (Table 2).

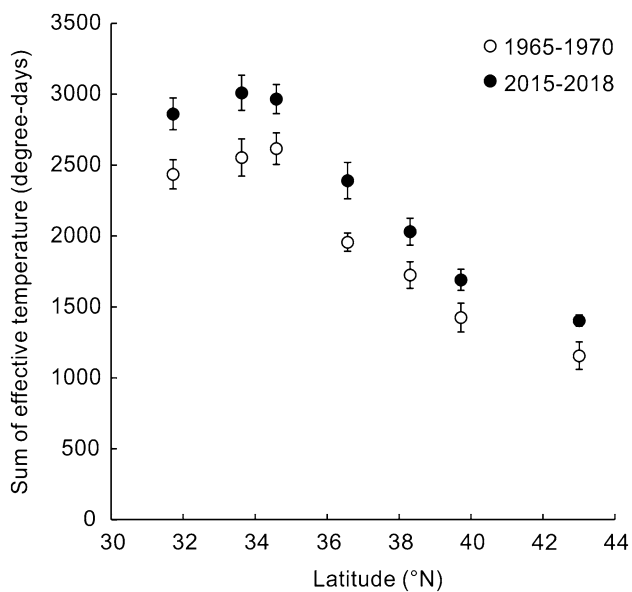
**Comparison of the sum of effective temperatures**

The growing season length of *D. nigrofasciatus* was found to increase with climate warming and decrease with increasing latitude. The sum of effective temperature was greater in 2015–2018 than in 1965–1970 by approximately 200–400 degree-days at each site. The sum of effective temperatures gradually decreased from 35°N to 43°N, although this trend became unclear at latitudes lower than 35°N both in 1965–1970 and 2015–2018 (Fig. 4).

**Table 2** A generalized additive model to test the effect of variables on the head width of adult *Dianemobius nigrofasciatus*

Variable	Estimate	SE	t value	P value
<b>Parametric coefficient</b>				
Intercept	1.769483	0.0044	400.892	<0.001
Sex (male)	-0.129294	0.0062	-20.818	<0.001
Period (1965–1970)	-0.004175	0.0104	-0.400	0.690
Sex × period	0.003382	0.0144	0.235	0.814
Variable	Effective df	F value	P value	
<b>Smooth terms</b>				
Latitude	7.754	23.64	<0.001	
Year	$3.671 \times 10^{-7}$	0.00	0.513	

The insects were collected from different latitudes in two periods, namely, 1965–1970 and 2015–2018  
df degrees of freedom



**Fig. 4** Comparison of the sum of effective temperatures from spring to autumn for development of *Dianemobius nigrofasciatus* between 1965–1970 and 2015–2018 at seven sites along the latitudinal gradient (mean  $\pm$  SD). The lower threshold for development was assumed to be 10 °C

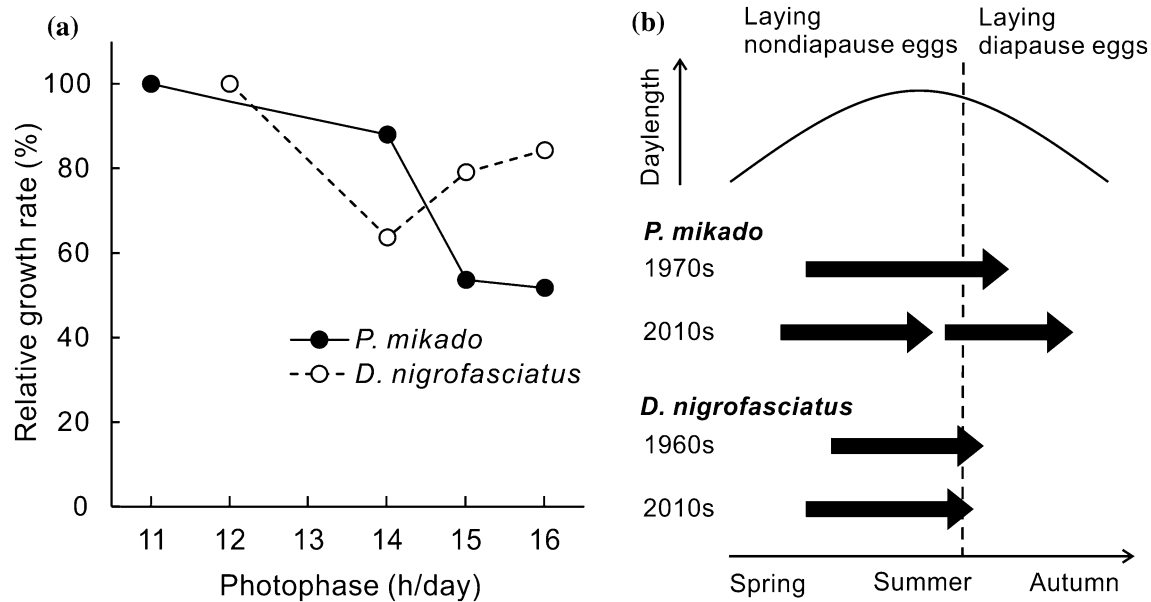
## Discussion

We found that adult *D. nigrofasciatus* collected in 2015–2018 exhibited a latitudinal saw-tooth cline in their head width, as did those collected in 1965–1970 (Fig. 3). The sampling dates were thought to be appropriate, because the C.V. of the head width was largest around the middle segment of the saw-tooth cline, suggesting that small bivoltine and large univoltine individuals coexisted there (Fig. S1). These clines indicate that the univoltine and bivoltine life cycles have prevailed at approximately 40–44°N and 31–37°N, respectively, and have been intermingled at approximately 37–40°N under the recent climate conditions. However, the lower and upper turning points of the saw-tooth cline of the head width were approximately 37°N and 40°N in recent years, respectively, and were different by less than 1° from five decades ago (Fig. 3), although the length of the growing season substantially increased during this time span due to climate warming (Fig. 4). Moreover, neither the sampling period nor its interaction with the latitude of the sampling site had a significant effect on the head width (Table 2), supporting the conclusion that the head width was not different between recent years and five decades ago within the same latitudinal range. We concluded, therefore, that the latitudinal distribution of the bivoltine life cycle remained unchanged over the last five decades in *D. nigrofasciatus*. The latitudinal variation in the sum of effective temperature five decades ago suggested that in *D.*

*nigrofasciatus*, approximately 1000 and 2000 degree-days are necessary for univoltine and bivoltine life cycles to be completed, respectively (Fig. 4), as described by Masaki (1972). The two life cycles also appeared to coexist at around 38°N in recent years, as they did five decades ago, even though the sum of effective temperature has reached 2000 degree-days there in the recent years. These results showed that a latitudinal variation in insect voltinism is not necessarily affected by an increase in the growing season length due to climate warming.

It is also noteworthy that a direct effect of climate warming on the head width of *D. nigrofasciatus* was not observed by comparison between the widths in recent years and five decades ago (Fig. 3, Table 2). This finding contrasts with proposed decreases in body size as a universal response to climate warming in organisms (Gardner et al. 2011; Sheridan and Bickford 2011). Some multispecies studies showed an increase, a decrease, or stability in body size in relation to climate warming in beetles and salamanders (Baar et al. 2018; Caruso et al. 2015; Tseng et al. 2018). These results indicate that some species-specific factors determine the direction and magnitude of its body size response to climate warming. In *D. nigrofasciatus*, it is possible that the negative effect of increasing temperature on the body size might be compensated by the positive effect of the longer growing season due to climate warming (Buckley et al. 2015), resulting in the apparent stability in body size. Even if the number of annual generations does not increase, this species might take advantage of longer growing seasons by increasing its reproductive period. Summarizing these results, we can conclude that the latitudinal variation in voltinism of *D. nigrofasciatus* is robust to climate warming.

In contrast, the closely related cricket *P. mikado* showed a latitudinal saw-tooth body size cline, of which the lower and upper turning points had shifted northward by 1°–2° from the 1970s to the 2010s (Matsuda et al. 2018). Moreover, the C.V. of its head width was largest around the middle segment of the saw-tooth cline in the 2010s, showing that univoltine and bivoltine life cycles were intermingled there. Taking these findings all together, it was concluded that the proportion of bivoltine individuals had increased at the middle latitude in *P. mikado* over the last four decades (Matsuda et al. 2018). It is a novel discovery that the change of the voltinism pattern over several decades was quite different between these two species, even though they have similar life cycles and geographic distributions, and are in the same tribe, Pteronemobiini. The latitude and altitude of the sampling sites, number of the sites and the samples per site were not quite different between the two studies. Photoperiodic regulation of nymphal development time is involved in the variable voltinism of some insects, including these two crickets (Lindestad et al. 2019; Masaki 1972, 1979). The different phenological response to climate warming might be explained by the different photoperiodic



**Fig. 5** Possible involvement of photoperiodic regulation of nymphal growth rate in the phenological change over several decades in *Polionemobius mikado* and *Dianemobius nigrofasciatus*. **a** Nymphal growth rate of populations relative to the rate under 11 h photoperiod in *P. mikado* and under 12 h photoperiod in *D. nigrofasciatus*. The growth rate is calculated as the percentage of development per day from hatching to adult emergence. Nymphs of *P. mikado* and

*D. nigrofasciatus* originated from adults collected in the 1970s and 1960s at 34–35°N and 37–38°N, respectively, where the univoltine and bivoltine life cycles were intermingled (modified from Masaki 1972, 1979). **b** Schematic representation of a temporal change in the growing season length and voltinism in the two species. Arrows indicate duration of the nymal stage

regulation of nymphal growth rate described above (Fig. 5a). If hatching of the overwintering generation becomes earlier due to climate warming in both of these species, nymphs of the overwintering generation will spend longer periods under intermediate daylengths, under which the nymphal growth rate is high in *P. mikado* and low in *D. nigrofasciatus*. As a result, summer adult emergence of *P. mikado* will become earlier, favoring the bivoltine life cycle in regions where it coexists with the univoltine one; whereas that of *D. nigrofasciatus* will remain unchanged (Fig. 5b). This can explain the results in *D. nigrofasciatus* and *P. mikado*, although it assumes that the photoperiodic regulation of growth rate has not changed in recent years. Further studies focusing on the life-history variations should help to reveal the factor(s) determining the response of voltinism to climate warming.

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