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Latitudinal cline of larval growth rate and its proximate mechanisms in a rhinoceros beetle

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Abstract

1. Juvenile growth rate is a key life-history trait with a major effect on various fitness components. Duration of the growing season changes with latitude, often resulting in latitudinal variations in growth rate. While many studies have shown a latitudinal cline of growth rate, most have used linear measurements of growth rate without considering the nonlinear nature of growth trajectories. Furthermore, elucidation of the proximate mechanisms causing increased growth rates would provide a fundamental understanding of the evolutionary process of the latitudinal cline of growth rates, which are largely unknown.

2. We used common garden experiments to examine the latitudinal variation of growth rate. We analysed the larval growth curve of 14 populations of the univoltine Japanese rhinoceros beetle *Trypoxylus dichotomus* (Coleoptera: Scarabaeidae) found along a 2,000-km latitudinal gradient. To clarify the mechanisms responsible for the latitudinal cline of growth rate, we compared food consumption and growth efficiency (i.e. the capacity to convert food into biomass) using three populations at high, middle and low latitudes.

3. There was a strong positive correlation between growth rate and latitude and a strong negative correlation between age at the inflexion point of the growth curve and latitude, indicating that larvae from northern populations grew more rapidly and reached the inflexion point earlier than those from southern populations.

4. The food intake increased linearly towards higher latitude. The growth efficiency of larvae from middle latitude was greater than that of larvae from low latitude, but there was no difference in the growth efficiency between high- and middle-latitude populations.

5. The increased growth rate at higher latitude is probably a local adaptation to complete development and growth during the short growth season. The rapid growth rate at higher latitudes could be explained by both the increased food consumption and the growth efficiency. However, the growth efficiency is probably maximized in the middle-latitude population, suggesting that some physiological costs prevent further increase in growth efficiency at higher latitudes. This study

provides compelling evidence for latitudinal cline of juvenile growth rate and disentangles the contributions of food intake and growth efficiency to the cline.

1 | INTRODUCTION

Growth rate is a key life-history trait with a major impact on various fitness components of individuals, such as survival and reproduction (Dmitriew, 2011). In ectothermic organisms, faster growth is thought to confer advantages including larger final body size and earlier maturation, resulting in lower predation risk (Abrams & Rowe, 1996; Arendt & Wilson, 1999; Stoks, Block, Meutter, & Johansson, 2005; Urban, 2008) and increased chances of reproduction (Blanckenhorn & Demont, 2004; Rowe & Ludwig, 1991). However, the intrinsic growth rate often varies among populations, suggesting that slower than maximal growth within physiological constraints is favoured under certain conditions (Dmitriew, 2011; Gotthard, 2001). Although the costs of fast growth remain insufficiently known, some studies have demonstrated short-term (e.g. higher mortality associated with the increase in resource acquisition effort; Abrams & Rowe, 1996; Gotthard, 2000; Stoks et al., 2005) and long-term costs (e.g. increased susceptibility to disease due to trade-offs between growth and immune responses; De Block & Stoks, 2008; Lee, Monaghan, & Metcalfe, 2013; Xie et al., 2015) associated with accelerated growth. The intrinsic growth rate is therefore determined by the net benefits gained by fast/slow growth rate (Abrams, Leimar, Nylin, & Wiklund, 1996; Arendt, 1997; Gotthard, 2001); this is diversified across populations as a result of the geographic variation of ecological factors such as the predation risk of foraging, food availability and time constraints (Dmitriew, 2011; Gotthard, 2001).

As temperature usually changes with latitude, the growth season of ectothermic organisms varies across latitudinal gradients. In particular, univoltine species have to complete development and growth within one growing season (Śniegula & Johansson, 2010). Therefore, an increased growth rate, due to seasonal time constraints, should be expected in high-latitude populations. Many studies have demonstrated a positive relationship between latitude and intrinsic growth rate in fishes (Conover, Brown, & Ehtisham, 1997; Conover & Present, 1990), amphibians (Laugen, Laurila, Räsänen, & Merilä, 2003; Lindgren & Laurila, 2005) and insects (Arnett & Gotelli, 1999; Blanckenhorn et al., 2018; Robinson & Partridge, 2001; Välimäki, Kivelä, Mäenpää, & Tammaru, 2013) with common garden experiments. However, the relationship between latitude and growth rate is not consistent in insects. Low-latitude populations of some species exhibit more generations per year than high-latitude populations, and consequently have less time available for growth (Roff, 1980). In such cases, higher growth rate is favoured at low latitudes

(Nygren, Bergström, & Nylin, 2008; Shama, Campero-Paz, Wegner, Block, & Stoks, 2011; Stoks, Swillen, & De Block, 2012).

The majority of previous studies on latitudinal cline in insect growth rate calculated growth rate by dividing the final body size by the developmental time (integral linear growth rate; Nygren et al., 2008; Välimäki et al., 2013). However, the growth trajectories of insects are nonlinear and discontinuous; thus, utilizing integral linear measures may confound the interpretation of the experimental results (Meister, Esperk, Välimäki, & Tammaru, 2017; Tammaru, Esperk, Ivanov, & Teder, 2010). To solve this problem, differential (instantaneous) growth rate (i.e. short-term mass increments at a specific phase of development) has been recently used in some cases (Meister et al., 2017; Stoks et al., 2012; Tammaru et al., 2010). Although this approach has several advantages over the linear integral measurements (Meister et al., 2017), differential growth measures based solely on a specific stage do not necessarily represent overall growth patterns. If natural selection acts on various components of the shape of the growth curve, approximating a nonlinear growth curve would be preferred to describe the growth trajectories. However, the measures of nonlinear fitting have rarely been used to assess the geographic variation of growth rate (Arnett & Gotelli, 1999).

The proximate mechanisms underlying latitudinal growth rate variation are less studied than the latitudinal growth rate variation per se. The rapid juvenile growth of populations at higher latitudes can mainly be achieved by two mechanisms (Present & Conover, 1992). One of them is an increased somatic growth efficiency (i.e. the capacity to convert ingested food to biomass) and the other is an increased food consumption rate. The latitudinal cline of growth efficiency has been reported in some species such as the fruit fly *Drosophila melanogaster* (Robinson & Partridge, 2001), the damselfly *Ischnura elegans* (Stoks et al., 2012), the Atlantic silverside *Menidia menidia* (Billerbeck, Schultz, & Conover, 2000; Present & Conover, 1992), the Atlantic halibut *Hippoglossus hippoglossus* (Jonassen et al., 2000) and the common frog *Rana temporaria* (Lindgren & Laurila, 2005). On the other hand, the latitudinal cline of food consumption has been reported in only a few species including *M. menidia* (Present & Conover, 1992) and *I. elegans* (Stoks et al., 2012). The two mechanisms are associated with different types of cost (Angilletta, Wilson, Navas, & James, 2003). For instance, increased growth efficiency is likely to reduce immune function and energy storage (Scharf, Filin, & Ovadia, 2009; Stoks, Block, Slos, Doorslaer, & Rolff, 2006) and increase oxidative stress (De Block & Stoks, 2008) via resource allocation trade-offs, whereas increased food consumption enhances the risk of predation when foraging activity is conspicuous to predators (Gotthard, 2000; Stoks et al., 2012).

The interspecific difference in underlying mechanisms of variation in growth rates could reflect the difference in ecology, as well as the types of physiological, behavioural and developmental trade-offs (Angilletta et al., 2003). Thus, the elucidation of the mechanisms causing increased growth rates provides a fundamental understanding of not only the processes behind the local adaptation of growth rates but also the selective forces or trade-offs determining the optimal growth rate in a population. However, the general pattern of the proximate mechanisms of increased growth rate remains unclear because there are limited studies on the topic, especially in invertebrates.

This study investigated the latitudinal cline of intrinsic growth rate and its underlying mechanisms in the rhinoceros beetle *Trypoxylus dichotomus* (Linnaeus, 1771; Coleoptera: Scarabaeidae), using common garden experiments. This species is strictly univoltine over its whole distribution range, which allows us to test for the effect of time constraints on larval growth rate across broad latitudes. The eggs of this species hatch in the summer and its larvae pupate early next summer (Figure 1A). In central Japan, larvae enter winter diapause in November and their growth ceases until March (Plaistow, Tsuchida, Tsubaki, & Setsuda, 2005). Their adult body size is mainly influenced by the time available for feeding prior to the onset of the

diapause (Plaistow et al., 2005). Considering the effect of seasonal time constraints, selection may favour faster growth during the early larval stage at higher latitudes where winter comes earlier. The body weight remains nearly constant during the latter half of the larval stage (approximately 100 days, Figure 1B; Johns, Gotoh, McCullough, Emlen, & Lavine, 2014; Plaistow et al., 2005). Such a growth trajectory (i.e. prolonged duration of the final instar of larvae) is not unique among scarab beetles (Christiansen, 2013; Vendl, Sípek, Kouklík, & Kratochvíl, 2018). Owing to this characteristic growth pattern of *T. dichotomus*, the linear integral measures of growth rate are unreliable. Thus, first we fitted a nonlinear growth curve model to estimate growth parameters and then examined the latitudinal cline of those parameters. In this analysis, we included 12 native populations along a 2,000-km latitudinal gradient and 2 non-native populations that were introduced during 1940–1960 to the region, 200 km north of the northern limit of their natural distribution from Honshu, the main island of Japan (Figure 2; Hokkaido Government, 2010). Although the exact origin of the introduced populations is unknown, they could provide an opportunity to explore how rapidly larval growth patterns adapt to novel environments. Second, we compared the differential measures of growth rate among three native populations of different
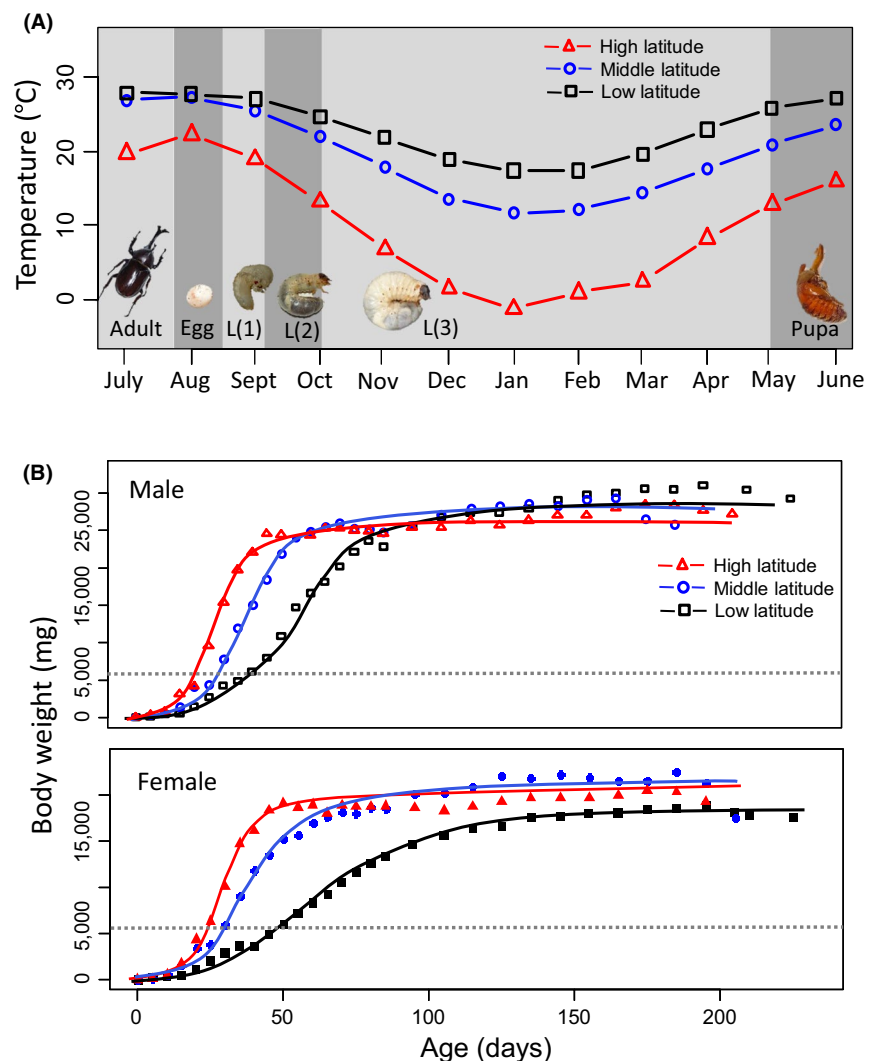
FIGURE 1 Life cycle of *Trypoxylus dichotomus*. (A) Mean monthly temperatures in Aomori (high latitude; triangles), Yakushima (middle latitude; circles) and central Taiwan (low latitude; squares) are shown. See Table S1 for the mean monthly temperature of other sites. The inset is the typical life cycle of *T. dichotomus* in Japan and Taiwan. L(n) represents *n*th instar larvae. (B) Typical growth trajectories and predicted growth curves by Gompertz models under common garden conditions of male (upper) and female (below) larvae from Aomori (triangles), Yakushima (circles) and central Taiwan (squares). The dotted line indicates the larval stage at which Experiment 2 (measurement of differential growth rate) was initiated
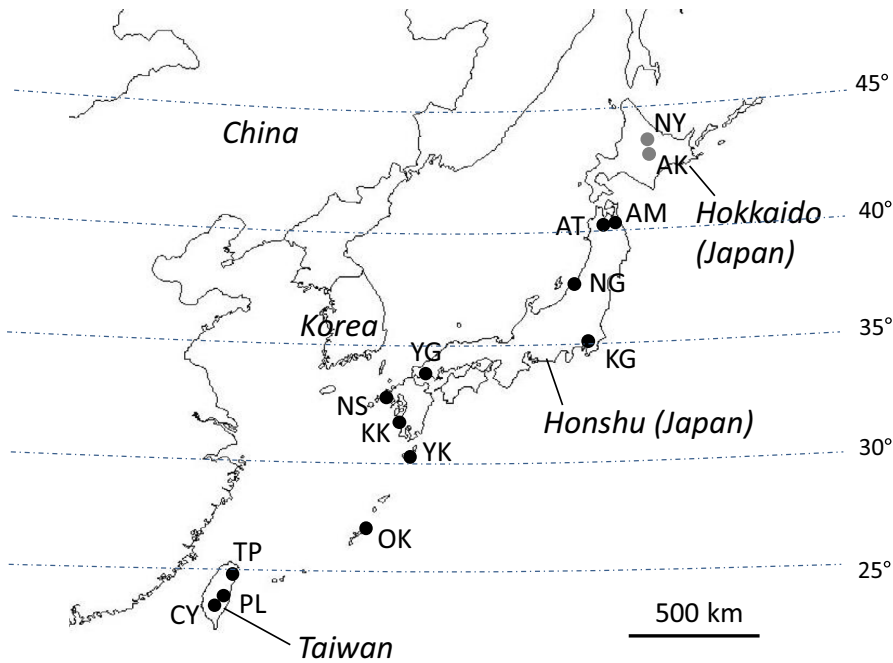
FIGURE 2 Map of East Asia showing the geographic origins of *Trypoxylus dichotomus* used in the growth curve analyses (Experiment 1). See Table 1 for abbreviations of population names and additional information about the localities. Introduced and native populations are indicated by grey and black dots, respectively

latitudinal regions (high, middle and low) to ensure the robustness of the results based on the nonlinear measures. Finally, we tested whether somatic growth efficiency and amount of food consumption vary across latitudes to assess the proximate mechanisms underlying the divergence of growth rate.

2 | MATERIALS AND METHODS

2.1 | Life cycle of *T. dichotomus*

This species is distributed in East Asia including Korea, Southeast China, Japan and Taiwan. The northern limit of its native distribution is Aomori, Japan. The typical life cycle of this species in Japan and Taiwan is shown in Figure 1A. This species is completely univoltine and does not display plasticity in phenology depending on developmental conditions. The females lay eggs in soil in July and August. The larvae inhabit the humus soil layer and feed on decaying organic matter. The larvae of populations in central Japan moult into the first and second instars at 15 and 35 days after hatching, respectively. The duration of the last (3rd) instar is 150–200 days (Hoshizaki, 2019; Johns et al., 2014). They overwinter as larvae and pupate early next summer.

2.2 | Common garden experiments

We conducted two experiments (Experiments 1 and 2) to calculate two types of growth rate measurements: (a) growth curve parameters throughout almost the entire larval stage and (b) differential growth rate on the short term (5 days) at the earlier part of the 3rd instar. In Experiment 2, we concurrently measured gross growth efficiency and amount of food consumed during the 5 days.

2.2.1 | Experiment 1: Estimation of growth curve parameters

Two introduced and 12 native populations of *T. dichotomus* found along a 2,000-km latitudinal gradient (from 23.5°N to 44.4°N) across Japan and Taiwan were used for assessing larval growth trajectories. Detailed information on the locations of the studied populations is shown in Table 1. The mean monthly temperature of the locations of the studied populations is shown in Table S1 and partly in Figure 1A. The altitude of the locations was 20–300 m. We collected eggs from three to six field-caught females, or F1 females, selected from strains established from several wild females for each population. However, only one female was available from the Akita population. Egg collection and weight measurement of hatched larvae were conducted following the procedure described in Kojima (2015). The females were individually introduced into a plastic cage with fermented sawdust as oviposition substrate and insect jellies sold commercially for rearing sap-feeding beetles. Eggs were collected 2 weeks later. Approximately 10–20 eggs per female were randomly chosen and used for this experiment. If the number of eggs were below 10, two more weeks were given to the females to lay more eggs. The eggs were put on wet tissue papers and checked every day until hatching. The hatched larvae were weighed and individually introduced into 430 ml cylindrical plastic containers (13 cm diameter × 7 cm height) filled with fermented sawdust commercially sold for rearing rhinoceros beetles (Dorcus Owner's shop, Osaka, Japan). The containers were refilled every 2 weeks with fresh sawdust. The sex of the larvae was identified by the morphology of the 9th abdominal segment during the 3rd larval instar (Ando, 2017; >98% accuracy, W. Kojima, pers. obs.). Male larvae were transferred to 860-ml cylindrical plastic containers (13 cm diameter × 15 cm height) at approximately 120 days after hatching to secure more space for pupation. The experiment was conducted

TABLE 1 Information on localities and status of studied populations of *Trypoxylus dichotomus*. The number of larvae (females, F and males, M) used in growth curve analysis is also shown

Population (abbreviation)	Latitude (°N)	Longitude (°E)	Locality	Status	Sample size (F, M)
Nayoro (NY)	44.4	142.5	Nayoro City, Hokkaido, JP	Introduced	20, 27
Asahikawa (AK)	43.7	142.5	Asahikawa City, Hokkaido, JP	Introduced	30, 38
Aomori[a] (AM)	40.7	141.4	Misawa City, Aomori, JP	Native	27, 28
Akita (AT)	39.7	140.7	Senboku City, Akita, JP	Native	12, 9
Niigata (NG)	38.5	139.3	Awashima, Niigata, JP	Native	17, 14
Kanagawa (KG)	35.6	139.5	Kawasaki City, Kanagawa, JP	Native	37, 37
Yamaguchi (YG)	34.2	131.5	Yamaguchi City, Yamaguchi, JP	Native	26, 39
Nagasaki (NS)	32.8	128.8	Fukue-jima, Nagasaki, JP	Native	17, 24
Kamikoshiki (KK)	31.8	129.9	Kamikoshiki-jima, Kagoshima, JP	Native	19, 20
Yakushima[b] (YK)	30.3	130.7	Yakushima, Kagoshima, JP	Native	40, 41
Okinawa (OK)	26.7	128.2	Okinawa-Island, Okinawa, JP	Native	36, 28
Taipei (TP)	25.0	121.5	New Taipei City, TW	Native	18, 16
Puli[c] (PL)	24.0	120.9	Puli Township, Nantou, TW	Native	26, 29
Chiayi[c] (CY)	23.5	120.5	Chiayi City, TW	Native	21, 23

Note: Superscripts a, b and c in the population name correspond to high-, middle- and low-latitude populations in Experiment 2, respectively.

at 25 ± 0.5°C, close to the ambient temperature this species usually experiences in the field during its earlier larval developmental stage (e.g. in August and September; Figure 1A; Table S1). The body weight of the larvae was measured every 5 days until they were 85-days old. As the daily growth increment of larvae gradually decreased as they aged (Figure 1B; Johns et al., 2014), their body mass was recorded every 10 days beginning at 85-days old and until the date of prepupation (i.e. the pupal cell building stage). Pupal weight was also measured approximately 10 days after pupation.

To estimate the growth curve parameters, we applied Gompertz and logistic models to each individual. These models are commonly used to analyse the growth trajectories in insects (Grunert, Clarke, Ahuja, Eswaran, & Nijhout, 2015; Lecheta & Moura, 2019; Newton & Doxon, 1990; Nijhout & Wheeler, 1996; Phoofolo, Elliott, & Giles, 2009) including Dynastinae species (Vendl et al., 2018) related to *T. dichotomus*. The Gompertz model was defined as follows:

$$\text{Body mass} = a \times e^{-e^{-k(\text{time}-l)}},$$

and the logistic model as follows:

$$\text{Body mass} = \frac{a}{1 + e^{-k(\text{time}-l)}},$$

where k is the growth rate, l is the age at the inflexion point and a is the asymptotic body mass. The Gompertz and logistic models have a fixed inflexion point, and the body mass at the inflexion point is 37% and 50% of the asymptotic body mass, respectively. The fitting of the growth curve was conducted using data of the initial 150 days of the larval stage during which all larvae of all populations attained nearly maximum size (>90% of asymptotic body mass). The reason we did not analyse growth during the full larval stage was because the larval body mass often begins to decrease at the end of the last instar (Figure 1B; Johns et al., 2014), which can lead to an unreliable estimation of growth curve parameters. Akaike's information criterion (AIC) was calculated to compare the goodness of fit between the Gompertz and logistic models. The growth parameters k, l and a and the pupal body mass were used for further statistical analyses.

2.2.2 | Experiment 2: Estimation of differential growth rate, growth efficiency and food consumption

We estimated the differential (instantaneous) growth rate, gross growth efficiency and food intake during a short period (5 days) using populations from three regions with different latitudes. Aomori, Yakushima and Taiwan (Puli and Chiayi) populations were used as high-, middle- and low-latitude populations, respectively. At the early stage of the 3rd instar larvae, 5.2–5.6 g was used at the start

of experiment, due to three reasons. First, they were in the rapid growth stage (Figure 1B). Second, as the duration of the 3rd instar is much longer than the duration of the 1st and 2nd instars, the body weight of the early stage of the 3rd instar larvae was not affected by moulting events during the experiment (larval body weight slightly decreased approximately 1 day after and before larval moulting). Third, the size of the frass excreted by the larvae was much larger than that of sawdust grains (substrate), thus allowing us to separate the frass from the substrate easily by sifting. As the experimental period (5 days) was much shorter than the entire period of the 3rd instar, the growth rate during such a short period can be approximated as differential measures of growth rate (Meister et al., 2017).

The offspring of the adults obtained from Experiment 1 were used in Experiment 2. The egg collection and larvae rearing procedures were the same as described above. The number of larvae used was 45–70 from four to six females from each population. The larvae were individually introduced into 120-ml plastic containers filled with fermented sawdust. They were observed every day to record the timing of moulting that started at 15 days of age. The larval body mass was measured every day after the 2nd moulting. When the body mass of the 3rd instar larvae reached 5.2–5.6 g, the larvae were individually transferred to 430-ml cylindrical plastic containers (13 cm diameter × 7 cm height) filled with fermented sawdust sifted through a 2 × 2 mm stainless steel mesh. The larval weight (LW_i) and total weight of the containers (including the larva, sawdust and top; TW_i) were measured prior to the experiments. The containers were kept in an incubator with a relative humidity of 95%–100% and a temperature of 25 ± 0.2°C. Five days later, the total weight of the container (TW_f) was measured again. The larval body weight (LW_f) was also measured. The differential growth rate (DGR) was calculated, based on the method described by Tammaru and Esperk (2007), as

$$DGR = \frac{LW_f^{1/3} - LW_i^{1/3}}{t},$$

where t is the experimental period in days (5 days).

A schematic image of the wet mass budget of the experimental system is shown in Figure 3. As it was practically impossible to measure food consumption directly, food consumption was indirectly determined by the sum of the weight of frass, larval weight gain and food spent on metabolism. The sawdust in the containers was immediately sifted to collect larval frass in the end of the experimental period. The wet weight of the frass was measured. To estimate the water mass evaporated from the sawdust during 5 days, the plastic containers with fermented sawdust only (control containers, n = 10) were weighed and kept for 5 days in the incubator. The total weight of the containers was measured again. The mean value of the mass decrement during 5 days was used as evaporative water loss. The mean mass of evaporative water (0.521 ± SE 0.018 g) accounted for only approximately 0.22% of the initial food mass and did not vary greatly between the containers (range: 0.41–0.56 g). Thus, the variation in evaporative water between containers is probably negligible.

Weight loss of food through larval metabolism and weight gain of larvae were calculated as follows (Figure 3):

$$Food\ loss\ via\ metabolism = TW_f - TW_i - (Evaporative\ water\ loss),$$

and

$$Larval\ weight\ gain = LW_f - LW_i.$$

Cumulative food consumption (FC) and gross growth efficiency (GE) were calculated as

$$FC = (Larval\ weight\ gain) + (Frass\ weight) + (Food\ loss\ via\ metabolism).$$

and

$$GE = 100 \times \frac{Larval\ weight\ gain}{FC}.$$

FC and GE were used in the statistical analyses described in the following section.

2.3 | Statistics

We used mixed linear models to examine the relationships between latitude and growth traits. Growth curve parameters (k, l or a) or pupal weight were dependent variables. The fixed effects were latitude, sex and their interaction, and the random effects were
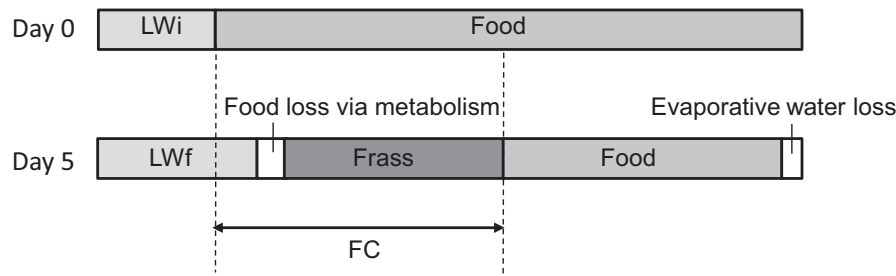
FIGURE 3 Schematic image of the wet mass budget of the experimental system. Some of the food ingested is excreted as frass and the remainder is assimilated. The food assimilated is spent on somatic growth and metabolism for various life-sustaining functions. The food used for metabolism is lost from the system as heat or gas (CO_2). LW_i, initial larval weight; LW_f, final larval weight. FC, food consumption

maternal identity and population identity. We also used simple linear regression of the mean values of growth parameters for each population of each sex to test the latitudinal cline of growth patterns. These analyses were conducted using only native populations.

The differential growth rate, food consumption and growth efficiency were compared among three populations using mixed ANCOVAs with maternal identity as a random effect. The fixed effects were population identity, sex and their interaction. We added initial body weight as a covariate. If the effect of population identity was significant in these models, pairwise comparison within sex was conducted using mixed ANCOVAs with Tukey methods. All analyses were carried out using R software, version 3.6.1 (R Development Core Team, 2019).

3 | RESULTS

### 3.1 | Latitudinal pattern of growth curve

We fitted two types of nonlinear growth models (Gompertz and logistic) for each larva. The better model with lower AIC was different among individuals, but the majority of larvae (81%) were better fitted to the Gompertz than the logistic model. Therefore, we conducted further analyses using the parameters estimated by the Gompertz model.

The results obtained from the mixed linear models showed that both growth rate k and age at the inflexion point l were significantly associated with latitude (Table 2). Simple regressions also showed that there was a strong positive correlation between k and latitude and a strong negative correlation between l and latitude (Figure 4; Table 3). These results suggest that larvae from northern population grew more rapidly and reached the inflexion point earlier than those from southern populations. The latitudinal variation is shown in Figure 1B that shows the typical growth trajectories of larvae from high, middle and low latitudes.

The growth rate of females was significantly higher than that of males, while females reached the inflexion point at a significantly younger age than males (Table 2). We found a significant interaction between latitude and sex for growth rate, suggesting that the effect of latitude on growth rate was greater in females than in males (Table 2; Figure 4). The interaction between sex and latitude was not significant for age at the
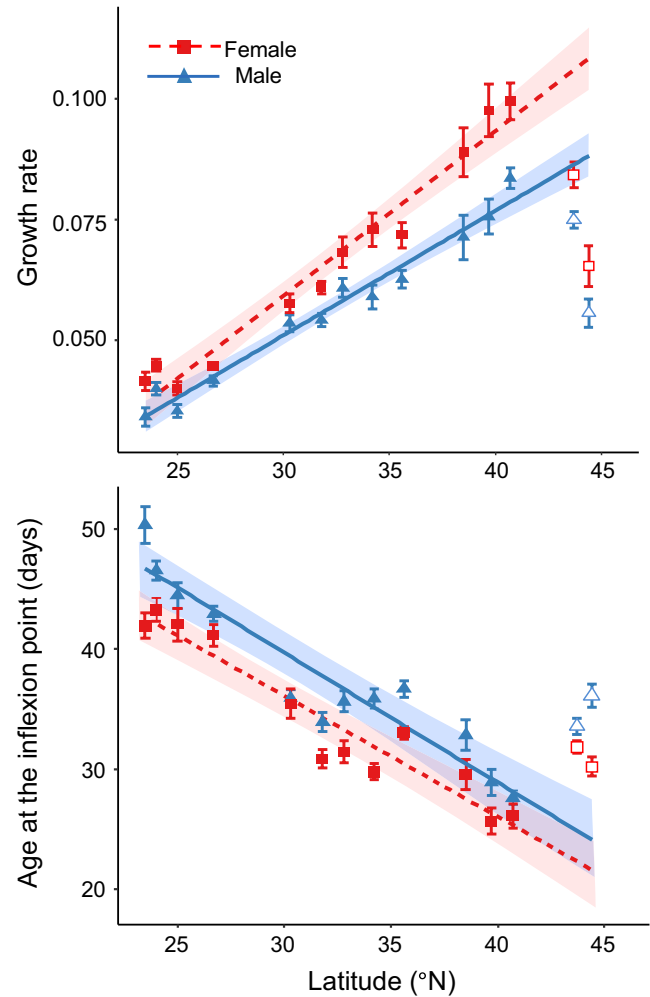
FIGURE 4 Relationship between mean (±*SE*) growth parameters (*k* and *l*) and latitudes of males (triangles) and females (squares) of *Trypoxylus dichotomus*. Regression lines and 95% confidence intervals estimated from native populations are shown. Filled and open points represent native and introduced populations, respectively

TABLE 2 Mixed linear model results for growth curve parameters and pupal weight of *Trypoxylus dichotomus*

Response variable	Predictor	df	F	p
k	Latitude	12.2	284.3	<0.001
	Sex	579.6	8.74	0.0032
	Latitude × Sex	578.7	21.5	<0.001
l	Latitude	10.94	111.5	<0.001
	Sex	525.3	6.04	0.0142
	Latitude × Sex	574	1.10	0.294
a	Latitude	10.40	6.66	0.0266
	Sex	579.0	38.9	<0.001
	Latitude × Sex	577.9	0.394	0.531
Pupal weight	Latitude	10.75	3.03	0.1101
	Sex	526.3	18.3	<0.001
	Latitude × Sex	525.4	0.436	0.509

TABLE 3 Pearson's correlation coefficients and *p* values between mean growth parameters and latitude of *Trypoxylus dichotomus*

Sex	Parameter	k	l	a	Pupal weight
Female	r	0.98	−0.96	−0.53	−0.73
	p	<0.001	<0.001	0.075	<0.01
Male	r	0.99	−0.95	−0.59	−0.33
	p	<0.001	<0.001	0.043	0.296

inflexion point. Figure 4 shows that both growth rate and age at the inflexion point of the two introduced populations from the north were obviously outside of the 95% confidence interval of the regression lines.

The asymptotic body mass *a* was negatively associated with latitude according to the results obtained from mixed linear models (Table 2), while simple regressions revealed that the latitudinal effect was significant in males but not in females (Table 3). The asymptotic body mass was larger in males than in females and the interaction between sex and latitude was not significant for the asymptotic body mass (Table 2).

The pupal body mass was significantly associated with sex, but not with latitude and the interaction between sex and latitude (Table 2). A simple regression revealed that the latitudinal effect on pupal weight was significant in females but not in males (Table 3).

3.2 | Inter-population variations in differential growth rate and physiological traits

Mixed ANCOVAs of differential growth rate and physiological traits (growth efficiency and food consumption) showed significant differences between populations (Table 4). All these response variables were significantly higher in males than in females (Figures 5 and 6; Table 4). The interaction between sex and population was not significantly associated with each response variable except for the food consumption (Table 4). The covariate, which was the initial body mass, was significantly associated with the food consumption but not with the differential growth rate and the growth efficiency.

In post-hoc multiple comparisons, a significant difference in differential growth rates was found among all combinations of populations for both sexes (Figures 5 and 6). The growth efficiency was

TABLE 4 Mixed ANCOVA results for the differential growth rate, growth efficiency and food consumption of *Trypoxylus dichotomus*

| Response variable	Predictor	df	F	p
Differential growth rate	Population	19.56	36.30	<0.001
	Sex	149.2	15.04	<0.001
	Population × Sex	148.7	1.84	0.162
	Initial mass	147.4	0.597	0.441
Growth efficiency	Population	11.44	42.94	<0.001
	Sex	163.4	20.47	<0.001
	Population × Sex	162.7	0.552	0.577
	Initial mass	163.7	0.061	0.805
Food consumption	Population	21.00	38.17	<0.001
	Sex	155.6	4.29	0.040
	Population × Sex	155.4	3.06	0.050
	Initial mass	157.0	1.60	0.207
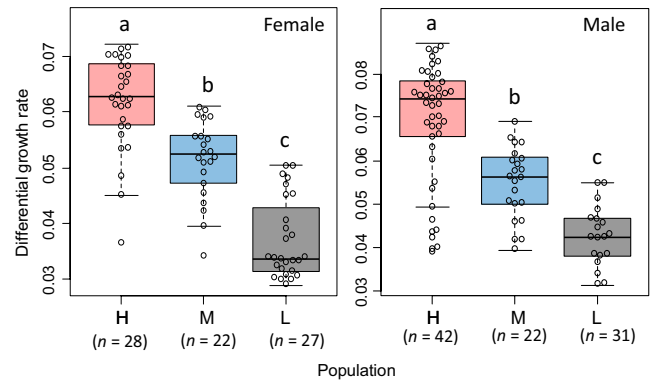
FIGURE 5 Differential growth rate of male (right) and female (left) larvae from high-latitude (H), middle-latitude (M) and low-latitude (L) populations of *Trypoxylus dichotomus*. Letters indicate significant differences at *p* < 0.05 according to the results of mixed ANCOVAs with a Tukey multiple comparison test within sexes
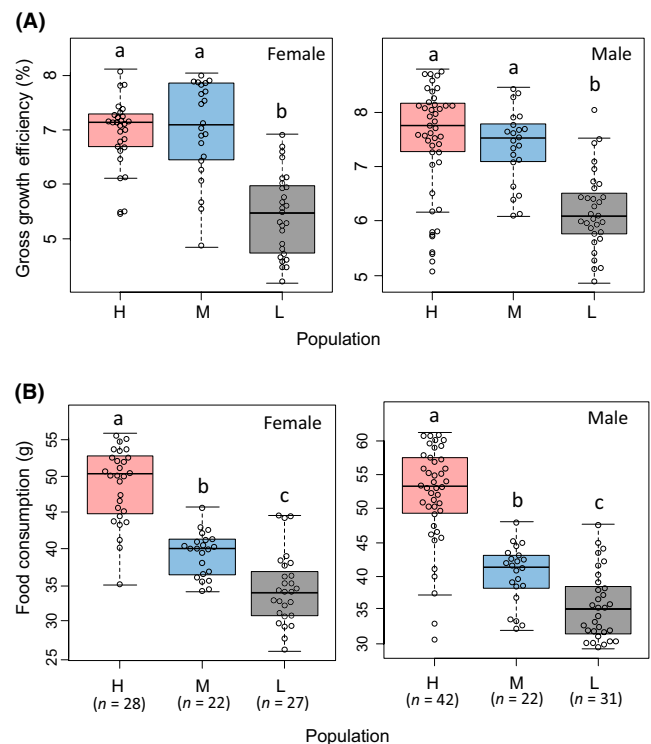
FIGURE 6 Gross growth efficiency (A) and food consumption (B) of male (right) and female larvae (left) from high-latitude (H), middle-latitude (M) and low-latitude (L) populations of *Trypoxylus dichotomus*. Letters indicate significant differences at *p* < 0.05 according to the results of mixed ANCOVAs with a Tukey multiple comparison test within sexes

significantly different between high- and low-latitude and between middle- and low-latitude populations for both sexes, but not significantly different between high- and middle-latitude populations (Figure 6A). The food consumption of both sexes was significantly different among all population combinations (Figure 6B). The relative contributions of food consumption and growth efficiency responsible for the differences in growth rate between populations are shown in Figure 7. The difference in growth rate between
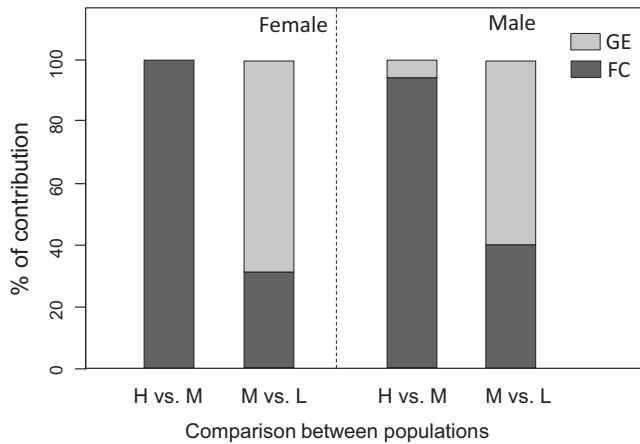
FIGURE 7 Relative contributions of food consumption (FC) and growth efficiency (GE) responsible for the differences in growth rates between populations (high [H] vs. middle [M] and M vs. low [L] latitudes) of *Trypoxylus dichotomus*. The relative contribution of FC was calculated as $100 \times \frac{\Delta FC}{\Delta FC + \Delta GE}$, where ΔFC and ΔGE are differences between populations in the means of FC and GE, respectively. The relative contribution of FC in males between high- and middle-latitude populations was calculated as 103% but shown as 100%

middle- and low-latitude populations is derived from both growth efficiency and food consumption, whereas the difference in growth rate between high- and middle-latitude populations is mainly derived from food consumption (Figure 7).

4 | DISCUSSION

Time constraint is thought to be one of the main selective forces responsible for geographic variation of growth rate in ectotherms (Blanckenhorn & Demont, 2004). Positive relationship between latitude and growth rate has been reported in univoltine species with less time available for growth in higher latitudes (Arnett & Gotelli, 1999; Blanckenhorn et al., 2018; Robinson & Partridge, 2001), and conversely, negative relationship reported in multivoltine species with more generations per year in lower latitudes (Nygren et al., 2008; Shama et al., 2011; Stoks et al., 2012). In this study, we examined latitudinal cline of growth rate of the obligate univoltine beetle *T. dichotomus* using growth curve analyses and differential growth rate, and further examined proximate mechanisms underlying the latitudinal cline. We found that larvae from higher-latitude populations grew more rapidly and reached the inflexion point earlier than those from lower-latitude populations. Although we cannot exclude the possibility that predation risk, food availability or other factors that correlate with latitude shape the latitudinal cline of growth rate, the rapid growth rate at higher latitudes is probably a local adaptation to complete development and growth during the short season. We also found that the food intake increased linearly towards higher latitudes. On the other hand, the growth efficiency increased with latitude, but reached plateau in middle latitude. The complex patterns highlight that the mechanisms of increased/decreased growth rates have been diversified even among populations within species.

Although a number of previous studies showed a latitudinal cline in the growth rates of insects, our results provide rigorous evidence for the following two reasons. First, our study employed 14 populations (including two introduced populations) across a broad latitudinal band (2,000 km). Previous studies have often compared growth rate among fewer than three populations (Arnett & Gotelli, 1999; Meister et al., 2017; Nygren et al., 2008; Robinson & Partridge, 2001; Shama et al., 2011; Śniegula & Johansson, 2010; Stoks et al., 2012). Using such a small number of populations may not allow for the detection of a nonlinear or discontinuous latitudinal cline (Välimäki et al., 2013). Second, our nonlinear fitting of growth curves provides detailed information about growth trajectories such as growth rate, age at the inflexion point and asymptotic body mass. Most previous studies have relied on integral measures of growth rate (dividing final size by developmental time) or differential growth rate (growth increment during a few days; Meister et al., 2017; Nygren et al., 2008; Śniegula & Johansson, 2010; Stoks et al., 2012; Välimäki et al., 2013), but these two measurements may confound the interpretation of the experimental results. For example, integral measures ignore the nonlinear characteristics of insect growth trajectories, and differential growth measures based on specific larval stage do not necessarily represent overall growth patterns (Meister et al., 2017). We are aware of only one study using growth curve parameters to examine the latitudinal pattern of growth rate in an antlion *Myrmeleon immaculatus*, in which a positive relationship between latitude and growth rate was shown (Arnett & Gotelli, 1999). We acknowledge that moulting was disregarded in the estimation of our parameters. The growth parameters could be better estimated based on the instar stage (Hoshizaki, 2019; Vendl et al., 2018); this is because growth physiology may be different among instars and the moulting process may interfere with the accurate estimation of the parameters (Tammaru et al., 2010).

The latitudinal cline of growth rate in native populations of *T. dichotomus* suggests local adaptation to seasonality. The feeding activity of larvae of this species ceases below, approximately, 10°C irrespective of the origin of the populations (W. Kojima, pers. obs., see also Plaistow et al., 2005). For example, while larvae in Aomori (northernmost native population) are expected to stop growing in October or November, larvae in Taiwan and Yakushima will probably continue to feed and develop throughout the duration of the larval stage (Figure 1A; Table S1). The adult body size is affected by the time available for feeding prior to the onset of winter diapause (Plaistow et al., 2005) and adult body size is an important fitness component in *T. dichotomus* (Hongo, 2007; Kojima, 2015). Moreover, the larger larval body size prior to winter probably results in higher survival rates during the winter diapause considering that a larger body size generally confers higher resistance to cold (Barron & Wilson, 1998; Krams, Daukšte, Kivleniece, Krama, & Rantala, 2011; Renault, Hance, Vannier, & Vernon, 2003; Smith, 2002). Thus, the rapid larval growth is obviously beneficial for the development of larvae at high latitudes.

We examined the larval growth rate of two non-native populations introduced further north than their natural distribution approximately 60–80 years ago. As the mean monthly temperature of Asahikawa is much lower than that of Aomori (Table S1), we expected a rapid

adaptation of the growth patterns of the introduced populations. In this study, we were unable to directly test whether any evolutionary changes occurred after introduction due to lack of knowledge on the origins of the source populations. However, the growth curve parameters (growth rate and age at the inflexion point) of the introduced populations deviated significantly from the regression lines estimated from native populations (Figure 4), indicating that the growth trajectories of the introduced populations are not fully adapted during the last 60–80 generations. This result contradicts previous studies in other ectotherms where rapid evolution of juvenile growth rate was detected in range-expanding or introduced populations (Phillips, 2009; Sargent & Lodge, 2014; Therry, Lefevre, & Stoks, 2014).

We found a negative relationship between asymptotic larval mass and latitude. Such a latitudinal cline in body size, known as the converse Bergmann's rule, has been reported in many organisms including insects (Blanckenhorn & Demont, 2004; Mousseau, 1997; Shelomi, 2012). This pattern is generally explained by the shorter time that is available for foraging, growth and development at higher latitudes (Blanckenhorn & Fairbairn, 1995; Chown & Klok, 2003; Horne, Hirst, & Atkinson, 2015; Kingsolver & Huey, 2008). However, according to the results of simple regression by sex, a significant latitudinal correlation was found only in males. Moreover, the pupal mass (a commonly used index of adult body size) was not significantly related to latitude. Overall, the converse Bergmann's rule was not strongly supported in *T. dichotomus*.

Our experimental thermal condition (25°C) was ecologically relevant, close to the natural thermal conditions during the earlier larval stage of *T. dichotomus* (in August and September) across a broad latitudinal range (Table S1). Our results, however, must be interpreted with caution. For example, the mean ambient temperature at the end of summer is lower than 25°C in some northern sites (e.g. Aomori, Akita and Niigata; Table S1). The physiological performance of insects, including their growth rate and efficiency, is plastic to thermal conditions (Robinson & Partridge, 2001; van Doorslaer & Stoks, 2005). The northern populations may adapt to the different temperatures, and optimal temperature for growth may be different from other populations. In addition, larvae in the laboratory experienced warmer conditions in the later part of the larval stage than they would have in natural conditions because our experiments were conducted at 25°C throughout the developmental stages. This warmer winter could cause changes in the later part of the growth patterns. In particular, larval duration might be longer, which would affect asymptotic larval mass (Nylin & Gotthard, 1998). Therefore, additional experiments under multiple thermal conditions, including simulated temperatures at the latitude of population origins, would improve the understanding of the latitudinal cline of life-history traits (Śniegula, Gołąb, & Johansson, 2016).

We found that the accelerated growth rate of northern population of *T. dichotomus* is attributable to both increased gross growth efficiency and food consumption. Increased growth efficiency may be achieved through an increase in the activity of digestive enzymes or the size of the digestive tract, as has been shown in amphibians (Lindgren & Laurila, 2005). According to previous studies in fishes (Billerbeck et al., 2000; Jonassen et al., 2000; Present & Conover, 1992), amphibians

(Lindgren & Laurila, 2005) and insects (Robinson & Partridge, 2001), increased gross growth efficiency is thought to be a more common mechanism for increased growth rate than increased food consumption. We present a rare example of latitudinal cline in food consumption (Present & Conover, 1992; Stoks et al., 2012). However, more importantly, pairwise comparisons among three populations (high, middle and low latitudes) showed complex patterns of the two proximate mechanisms. Specifically, food consumption, but not growth efficiency, was different between high- and middle-latitude populations. On the other hand, both mechanisms were responsible for the difference in growth rates between middle- and low-latitude populations. Growth efficiency seemed to be maximized in the middle-latitude population within physiological limitations. Increased growth efficiency may incur physiological costs, such as reduced immune function and energy storage via resource allocation (Scharf et al., 2009; Stoks et al., 2006). Growth efficiency may also be constrained by the size of the digestive tract (Laugen et al., 2003). The cost and constraints probably determine the upper limit of growth efficiency in *T. dichotomus*. This study disentangled the contributions of food intake and growth efficiency to the latitudinal cline in growth rate, adding to the list of studies on proximate mechanisms underlying latitudinal growth rate variation.

AUTHORS' CONTRIBUTIONS

W.K. and T.N. conceived the ideas and designed the methodology; W.K., T.N., A.F., C.-P.L., M.H., Y.H., A.K., S.S. and R.Y. performed the experiments; W.K., T.N. and C.-P.L. analysed the data and wrote the manuscript.

DATA AVAILABILITY STATEMENT

Data deposited in the Dryad Digital Repository https://doi.org/10.5061/dryad.tb2rbnzx9 (Kojima et al., 2020).

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REFERENCES

Abrams, P. A., Leimar, O., Nylin, S., & Wiklund, C. (1996). The effect of flexible growth rates on optimal sizes and development times in a seasonal environment. *The American Naturalist*, *147*, 381–395. https://doi.org/10.1086/285857

Abrams, P. A., & Rowe, L. (1996). The effects of predation on the age and size of maturity of prey. *Evolution*, *50*, 1052–1061. https://doi.org/10.1111/j.1558-5646.1996.tb02346.x

Ando, A. M. (2017). *Otonano field Zukan Gensyokude Tanoshimu Kabutomushi Kuwagatamushi Zukan Shiiku Guide* (in Japanese). Jitsugyo no Nihon Sha.

Angilletta, M. J., Wilson, R. S., Navas, C. A., & James, R. S. (2003). Tradeoffs and the evolution of thermal reaction norms. *Trends in Ecology & Evolution*, *18*, 234–240. https://doi.org/10.1016/S0169-5347(03)00087-9

Arendt, J. D. (1997). Adaptive intrinsic growth rates: An integration across taxa. *Quarterly Review of Biology*, *72*, 149–177. https://doi.org/10.1086/419764

Arendt, J. D., & Wilson, D. S. (1999). Countergradient selection for rapid growth in pumpkinseed sunfish: Disentangling ecological and evolutionary effects. *Ecology*, *80*, 2793–2798. https://doi.org/10.1890/0012-9658(1999)080[2793:CSFRGI]2.0.CO;2

Arnett, A. E., & Gotelli, N. J. (1999). Geographic variation in life-history traits of the ant lion, *Myrmeleon immaculatus*: Evolutionary implications of Bergmann's rule. *Evolution*, *53*, 1180–1188. https://doi.org/10.1111/j.1558-5646.1999.tb04531.x

Barron, A., & Wilson, K. (1998). Overwintering survival in the seven spot ladybird, *Coccinella septempunctata* (Coleoptera: Coccinellidae). *European Journal of Entomology*, *95*, 639–642.

Billerbeck, J. M., Schultz, E. T., & Conover, D. O. (2000). Adaptive variation in energy acquisition and allocation among latitudinal populations of the Atlantic silverside. *Oecologia*, *122*, 210–219. https://doi.org/10.1007/PL00008848

Blanckenhorn, W. U., Bauerfeind, S. S., Berger, D., Davidowitz, G., Fox, C. W., Guillaume, F., … Schäfer, M. A. (2018). Life history traits, but not body size, vary systematically along latitudinal gradients on three continents in the widespread yellow dung fly. *Ecography*, *41*, 2080–2091. https://doi.org/10.1111/ecog.03752

Blanckenhorn, W. U., & Demont, M. (2004). Bergmann and converse Bergmann latitudinal clines in arthropods: Two ends of a continuum? *Integrative and Comparative Biology*, *44*, 413–424. https://doi.org/10.1093/icb/44.6.413

Blanckenhorn, W. U., & Fairbairn, D. J. (1995). Life history adaptation along a latitudinal cline in the water strider *Aquarius remigis* (Heteroptera: Gerridae). *Journal of Evolutionary Biology*, *8*, 21–41. https://doi.org/10.1046/j.1420-9101.1995.8010021.x

Chown, S. L., & Klok, C. J. (2003). Altitudinal body size clines: Latitudinal effects associated with changing seasonality. *Ecography*, *26*, 445–455. https://doi.org/10.1034/j.1600-0587.2003.03479.x

Christiansen, P. (2013). Larval growth rates and sexual differences of resource allocation in the cetoniine scarab *Mecynorhina polyphemus* Fabricius 1781 (Coleoptera: Scarabaeidae: Goliathini). *Journal of Natural History*, *47*, 1287–1307. https://doi.org/10.1080/00222933.2012.763061

Conover, D. O., Brown, J. J., & Ehtisham, A. (1997). Countergradient variation in growth of young striped bass (*Morone saxatilis*) from different latitudes. *Canadian Journal of Fisheries and Aquatic Sciences*, *54*, 2401–2409. https://doi.org/10.1139/f97-147

Conover, D. O., & Present, T. M. (1990). Countergradient variation in growth rate: Compensation for length of the growing season among Atlantic silversides from different latitudes. *Oecologia*, *83*, 316–324. https://doi.org/10.1007/BF00317554

De Block, M., & Stoks, R. (2008). Compensatory growth and oxidative stress in a damselfly. *Proceedings of the Royal Society B: Biological Sciences*, *275*, 781–785. https://doi.org/10.1098/rspb.2007.1515

Dmitriew, C. M. (2011). The evolution of growth trajectories: What limits growth rate? *Biological Reviews*, *86*, 97–116. https://doi.org/10.1111/j.1469-185X.2010.00136.x

Gotthard, K. (2000). Increased risk of predation as a cost of high growth rate: An experimental test in a butterfly. *Journal of Animal Ecology*, *69*, 896–902. https://doi.org/10.1046/j.1365-2656.2000.00432.x

Gotthard, K. (2001). Growth strategies of ectothermic animals in temperate environments. In D. Atkinson & M. Thorndyke (Eds.), *Environment and animal development* (pp. 287–304). Oxford, UK: BIOS Scientific Publishers.

Grunert, L. W., Clarke, J. W., Ahuja, C., Eswaran, H., & Nijhout, H. F. (2015). A quantitative analysis of growth and size regulation in *Manduca sexta*: The physiological basis of variation in size and age at metamorphosis. *PLoS ONE*, *10*, e0127988. https://doi.org/10.1371/journal.pone.0127988

Hokkaido Government. (2010). *Database of invasive species in Hokkaido* (in Japanese). Retrieved from http://bluelist.pref.hokkaido.lg.jp/

Hongo, Y. (2007). Evolution of male dimorphic allometry in a population of the Japanese horned beetle *Trypoxylus dichotomus septentrionalis*. *Behavioral Ecology and Sociobiology*, *62*, 245–253. https://doi.org/10.1007/s00265-007-0459-2

Horne, C. R., Hirst, A. G., & Atkinson, D. (2015). Temperature-size responses match latitudinal-size clines in arthropods, revealing critical differences between aquatic and terrestrial species. *Ecology Letters*, *18*, 327–335. https://doi.org/10.1111/ele.12413

Hoshizaki, S. (2019). Catch-up growth in the rhinoceros beetle *Trypoxylus dichotomus* (Coleoptera: Scarabaeidae): Smaller neonates gain relatively more body mass during larval development. *Entomological Science*, *22*, 373–380. https://doi.org/10.1111/ens.12378

Johns, A., Gotoh, H., McCullough, E. L., Emlen, D. J., & Lavine, L. C. (2014). Heightened condition-dependent growth of sexually selected weapons in the rhinoceros beetle, *Trypoxylus dichotomus* (Coleoptera: Scarabaeidae). *Integrative and Comparative Biology*, *54*, 614–621. https://doi.org/10.1093/icb/icu041

Jonassen, T. M., Imsland, A. K., Fitzgerald, R., Bonga, S. W., Ham, E. V., Naevdal, G., … Stefansson, S. O. (2000). Geographic variation in growth and food conversion efficiency of juvenile Atlantic halibut related to latitude. *Journal of Fish Biology*, *56*, 279–294. https://doi.org/10.1111/j.1095-8649.2000.tb02106.x

Kingsolver, J. G., & Huey, R. B. (2008). Size, temperature, and fitness: Three rules. *Evolutionary Ecology Research*, *10*, 251–268.

Kojima, W. (2015). Variation in body size in the giant rhinoceros beetle *Trypoxylus dichotomus* is mediated by maternal effects on egg size. *Ecological Entomology*, *40*, 420–427. https://doi.org/10.1111/een.12205

Kojima, W., Nakakura, T., Fukuda, A., Lin, C.-P., Harada, M., Hashimoto, Y., … Yamamoto, R. (2020). Data from: Latitudinal cline of larval growth rate and its proximate mechanisms in a rhinoceros beetle. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.tb2rbnzx9

Krams, I., Daukšte, J., Kivleniece, I., Krama, T., & Rantala, M. J. (2011). Overwinter survival depends on immune defence and body length in male *Aquarius najas* water striders. *Entomologia Experimentalis et Applicata*, *140*, 45–51. https://doi.org/10.1111/j.1570-7458.2011.01132.x

Laugen, A. T., Laurila, A., Räsänen, K., & Merilä, J. (2003). Latitudinal countergradient variation in the common frog (*Rana temporaria*) development rates – Evidence for local adaptation. *Journal of Evolutionary Biology*, *16*, 996–1005. https://doi.org/10.1046/j.1420-9101.2003.00560.x

Lecheta, M. C., & Moura, M. O. (2019). Estimating the age of forensically useful blowfly, *Sarconesia chlorogaster* (Diptera: Calliphoridae), using larval length and weight. *Journal of Medical Entomology*, *56*, 915–920. https://doi.org/10.1093/jme/tjz028

Lee, W. S., Monaghan, P., & Metcalfe, N. B. (2013). Experimental demonstration of the growth rate–lifespan trade-off. *Proceedings of the Royal Society B: Biological Sciences*, *280*, 20122370. https://doi.org/10.1098/rspb.2012.2370

Lindgren, B., & Laurila, A. (2005). Proximate causes of adaptive growth rates: Growth efficiency variation among latitudinal populations of *Rana temporaria*. *Journal of Evolutionary Biology*, *18*, 820–828. https://doi.org/10.1111/j.1420-9101.2004.00875.x

Meister, H., Esperk, T., Välimäki, P., & Tammaru, T. (2017). Evaluating the role and measures of juvenile growth rate: Latitudinal variation in insect life histories. *Oikos*, *126*, 1726–1737. https://doi.org/10.1111/oik.04233

Mousseau, T. A. (1997). Ectotherms follow the converse to Bergmann's rule. *Evolution*, *51*, 630–632. https://doi.org/10.1111/j.1558-5646.1997.tb02453.x

Newton, C., & Dixon, A. F. G. (1990). Pattern of growth in weight of alate and apterous nymphs of the English grain aphid, *Sitobion avenae*. *Entomologia Experimentalis et Applicata*, *55*, 231–238. https://doi.org/10.1111/j.1570-7458.1990.tb01367.x

Nijhout, H. F., & Wheeler, D. E. (1996). Growth models of complex allometries in holometabolous insects. *The American Naturalist*, *148*, 40–56. https://doi.org/10.1086/285910

Nygren, G. H., Bergström, A., & Nylin, S. (2008). Latitudinal body size clines in the butterfly *Polyommatus icarus* are shaped by gene-environment interactions. *Journal of Insect Science*, *8*, 1–13. https://doi.org/10.1673/031.008.4701

Nylin, S., & Gotthard, K. (1998). Plasticity in life-history traits. *Annual Review of Entomology*, *43*, 63–83. https://doi.org/10.1146/annurev.ento.43.1.63

Phillips, B. L. (2009). The evolution of growth rates on an expanding range edge. *Biology Letters*, *5*, 802–804. https://doi.org/10.1098/rsbl.2009.0367

Phoofolo, M. W., Elliott, N. C., & Giles, K. L. (2009). Analysis of growth and development in the final instar of three species of predatory Coccinellidae under varying prey availability. *Entomologia Experimentalis et Applicata*, *131*, 264–277. https://doi.org/10.1111/j.1570-7458.2009.00849.x

Plaistow, S. J., Tsuchida, K., Tsubaki, Y., & Setsuda, K. (2005). The effect of a seasonal time constraint on development time, body size, condition, and morph determination in the horned beetle *Allomyrina dichotoma* L. (Coleoptera: Scarabaeidae). *Ecological Entomology*, *30*, 692–699. https://doi.org/10.1111/j.0307-6946.2005.00740.x

Present, T. M. C., & Conover, D. O. (1992). Physiological basis of latitudinal growth differences in *Menidia menidia*: Variation in consumption or efficiency? *Functional Ecology*, *6*, 23–31. https://doi.org/10.2307/2389767

R Development Core Team. (2019). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Renault, D., Hance, T., Vannier, G., & Vernon, P. (2003). Is body size an influential parameter in determining the duration of survival at low temperatures in *Alphitobius diaperinus* Panzer (Coleoptera: Tenebrionidae)? *Journal of Zoology*, *259*, 381–388. https://doi.org/10.1017/S0952836902003382

Robinson, S. J. W., & Partridge, L. (2001). Temperature and clinal variation in larval growth efficiency in *Drosophila melanogaster*. *Journal of Evolutionary Biology*, *14*, 14–21. https://doi.org/10.1046/j.1420-9101.2001.00259.x

Roff, D. A. (1980). Optimizing development time in a seasonal environment: The 'ups and downs' of clinal variation. *Oecologia*, *45*, 202–208. https://doi.org/10.1007/BF00346461

Rowe, L., & Ludwig, D. (1991). Size and timing of metamorphosis in complex life cycles: Time constraints and variation. *Ecology*, *72*, 413–427. https://doi.org/10.2307/2937184

Sargent, L. W., & Lodge, D. M. (2014). Evolution of invasive traits in nonindigenous species: Increased survival and faster growth in invasive populations of rusty crayfish (*Orconectes rusticus*). *Evolutionary Applications*, *7*, 949–961. https://doi.org/10.1111/eva.12198

Scharf, I., Filin, I., & Ovadia, O. (2009). A trade-off between growth and starvation endurance in a pit-building antlion. *Oecologia*, *160*, 453–460. https://doi.org/10.1007/s00442-009-1316-y

Shama, L. N., Campero-Paz, M., Wegner, K. M., De Block, M., & Stoks, R. (2011). Latitudinal and voltinism compensation shape thermal reaction norms for growth rate. *Molecular Ecology*, *20*, 2929–2941. https://doi.org/10.1111/j.1365-294X.2011.05156.x

Shelomi, M. (2012). Where are we now? Bergmann's rule sensu lato in insects. *The American Naturalist*, *180*, 511–519. https://doi.org/10.1086/667595

Smith, R. J. (2002). Effect of larval body size on overwinter survival and emerging adult size in the burying beetle, *Nicrophorus investigator*. *Canadian Journal of Zoology*, *80*, 1588–1593. https://doi.org/10.1139/z02-151

Śniegula, S., Gołąb, M. J., & Johansson, F. (2016). A large-scale latitudinal pattern of life-history traits in a strictly univoltine damselfly. *Ecological Entomology*, *41*, 459–472. https://doi.org/10.1111/een.12314

Śniegula, S., & Johansson, F. (2010). Photoperiod affects compensating developmental rate across latitudes in the damselfly *Lestes sponsa*. *Ecological Entomology*, *35*, 149–157. https://doi.org/10.1111/j.1365-2656.2005.00969.x

Stoks, R., Block, M. D., Slos, S., Doorslaer, W. V., & Rolff, J. (2006). Time constraints mediate predator-induced plasticity in immune function, condition, and life history. *Ecology*, *87*, 809–815. https://doi.org/10.1890/0012-9658(2006)87[809:TCMPPI]2.0.CO;2

Stoks, R., Block, M. D., Van De Meutter, F., & Johansson, F. (2005). Predation cost of rapid growth: Behavioural coupling and physiological decoupling. *Journal of Animal Ecology*, *74*, 708–715. https://doi.org/10.1111/j.1365-2656.2005.00969.x

Stoks, R., Swillen, I., & De Block, M. (2012). Behaviour and physiology shape the growth accelerations associated with predation risk, high temperatures and southern latitudes in *Ischnura* damselfly larvae. *Journal of Animal Ecology*, *81*, 1034–1040. https://doi.org/10.1111/j.1365-2656.2012.01987.x

Tammaru, T., & Esperk, T. (2007). Growth allometry of immature insects: Larvae do not grow exponentially. *Functional Ecology*, *21*, 1099–1105. https://doi.org/10.1111/j.1365-2435.2007.01319.x

Tammaru, T., Esperk, T., Ivanov, V., & Teder, T. (2010). Proximate sources of sexual size dimorphism in insects: Locating constraints on larval growth schedules. *Evolutionary Ecology*, *24*, 161–175. https://doi.org/10.1007/s10682-009-9297-1

Therry, L., Lefevre, E., Bonte, D., & Stoks, R. (2014). Increased activity and growth rate in the non-dispersive aquatic larval stage of a damselfly at an expanding range edge. *Freshwater Biology*, *59*, 1266–1277. https://doi.org/10.1111/fwb.12346

Urban, M. C. (2008). Salamander evolution across a latitudinal cline in gape-limited predation risk. *Oikos*, *117*, 1037–1049. https://doi.org/10.1111/j.0030-1299.2008.16334.x

Välimäki, P., Kivelä, S. M., Mäenpää, M. I., & Tammaru, T. (2013). Latitudinal clines in alternative life histories in a geometrid moth. *Journal of Evolutionary Biology*, *26*, 118–129. https://doi.org/10.1111/jeb.12033

Van Doorslaer, W., & Stoks, R. (2005). Growth rate plasticity to temperature in two damselfly species differing in latitude: Contributions of behaviour and physiology. *Oikos*, *111*, 599–605. https://doi.org/10.1111/j.1600-0706.2005.14335.x

Vendl, T., Sípek, P., Kouklík, O., & Kratochvíl, L. (2018). Hidden complexity in the ontogeny of sexual size dimorphism in male-larger beetles. *Scientific Reports*, *8*, 5871. https://doi.org/10.1038/s41598-018-24047-1

Xie, J., De Clercq, P., Pan, C., Li, H., Zhang, Y., & Pang, H. (2015). Physiological effects of compensatory growth during the larval stage of the ladybird, *Cryptolaemus montrouzieri*. *Journal of Insect Physiology*, *83*, 37–42. https://doi.org/10.1016/j.jinsphys.2015.11.001

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.