

# Geographic variation in body size of the migratory locust *Locusta migratoria* (Orthoptera, Acrididae): Masaki's cline and phase polyphenism

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## Abstract

Adults of the migratory locust *Locusta migratoria* (Linnaeus, 1758) were collected in the Japanese Archipelago, which extends from the Ryukyu subtropical region to the Hokkaido cool-temperate region, covering more than 2,500 km. A saw-toothed pattern was observed in body size along the latitudinal or annual mean temperature gradient, which is similar to Masaki's clines initially described for crickets. The latitudinal cline of locusts was also observed in the laboratory, suggesting that this cline was primarily due to genetic variation. In the northern univoltine zone, locust body size increased toward the south. The latitudinal size trend was reversed in the transitional zones where the voltinism shifted from univoltine to bivoltine and from bivoltine to trivoltine life cycles. These patterns may be explained by changes in the length of the growing season for development and reproduction. Body size varied with growth efficiency but not with the variable lengths of nymphal development. Larger females had more ovarioles and produced fatter egg pods containing more eggs per pod. The morphometric ratio, F/C (hind femur length/head width), tended to decrease with latitude, but this characteristic could be primarily due to phylogenetic differences between the northern and southern clades. It was confirmed that F/C ratio decreased when the locusts were reared in a group. The sexual size dimorphism, or SSD, tended to increase as the mean body sizes of populations increased, converse to Rensch's rule. The relative body size of females and males correlated with latitude and was greatly reduced when the insects were reared in a group. The smaller rate of increase at higher latitudes may be related to male–female associations and predation pressure.

## Keywords

adult head width, latitudinal cline, sexual size dimorphism, voltinism

## Introduction

The migratory locust, *Locusta migratoria* (Linnaeus, 1758), is distributed widely in the Old World, including the African, Eurasian, and Australian continents. Because of its economic importance, many studies have been performed on various aspects of this locust's basic and applied biology (Uvarov 1966, 1977).

Farrow and Colless (1980) analyzed numerous adult specimens collected worldwide and found large variation in body size and morphometric traits. Based on 31 solitarious populations, they attempted to uncover morphological characters that might describe groups of populations that could be designated as subspecies but found that morphometric variation within the geographic ranges of the eight putative subspecies was often as great as the variation between subspecies, providing no adequate basis for either sub-specific classification or determining the limits for populations of different geographic regions. They also concluded that locust populations showing different life cycles—univoltine vs. multivoltine—could not be distinguished on morphometric grounds alone. Adult specimens of this locust often show large variations in body size and morphometric characters in China and Japan (H. Tanaka 1982, A. Tanaka 1987, Kang et al. 1989, Tanaka and Zhu 2008, Yamagishi and Tanaka 2009, Tanaka 2022). However, the factors responsible for the geographic variation have not been identified, although they are partly caused by the phase polyphenism induced by crowding in the populations (Uvarov 1977, Farrow and Colless 1980, Pener 1991, Pener and Simpson 2009).

Body size has been found to strongly correlate with many physiological and fitness characteristics in insects (Roff 1980, Blanckenhorn 2000, Whitman 2008). Many insects vary geographically in adult body size. Several patterns of geographical clines are known. Some species follow Bergmann's rule in which body size increases at higher latitudes, while others exhibit a reversed Bergmann's rule, which is common in insects (Masaki 1967, Tanaka 1991, Blanckenhorn and Demont 2004, Blanckenhorn et al. 2006, Bidau and Marti 2008, Chown and Gaston 2010, Kivelä et al. 2011, Bidau et al. 2016). A more complicated pattern is known in species with variable life cycles. In two species of ground crickets, *Dianemobius nigrofasciatus* Matsumura (1904) and *Polionemobius taprobanensis* Walker (1869), Masaki (1973, 1978a, b, 1979, 1983) discovered a saw-toothed cline in body size along the latitudinal gradient of the Japanese Archipelago. In the northern area, body size increased toward the south, decreased in the central area, and

again increased in the more southern area of the distribution. Subsequently, Masaki reared crickets under various photoperiodic conditions and found that adult body size was a function of the duration of nymphal development. This result led him to suggest that the saw-toothed cline was a product of the local adjustment of nymphal development by means of photoperiodic response and genetic variation and could be explained by the relationship between voltinism and the heat available for the development of the cricket (Kidokoro and Masaki 1978, Masaki 1979, 1996, Masaki and Walker 1987, Walker and Masaki 1989). Since this discovery, the saw-toothed pattern has been reported in other species (Nylín and Svárd 1991, Johansson 2003, Kivelä et al. 2011) and has been analyzed from various points of view (Roff 1980, Tauber et al. 1986, Iwasa et al. 1994, Chown and Gaston 2010, Levy et al. 2015). Dingle (1993) proposed that this cline should be called 'Masaki's cline' because Masaki was the first to discover it.

In a previous study examining geographic variation in the body size of the migratory locust, we collected solitary specimens at six localities in China ranging from 47.4°N to 19.2°N, and we found a complicated pattern in head width along the latitudinal gradient (Tanaka and Zhu 2008). Although there was a possibility that the variation in adult body size was related to life cycles or voltinism, as observed in crickets (Masaki 1973, 1978a), the small sample size did not allow testing of this possibility in detail.

Migratory locusts commonly occur in the Japanese archipelago over 3,000 km south to north between 24°N and 45°N (Tanaka 1994). Recently, we analyzed the phylogenetic relationships among different migratory locust populations in the world by sequencing four mitochondrial DNA regions and discovered that the migratory locust consisted of two clades, the southern and northern clades (Tokuda et al. 2010). Tropical and subtropical populations from Africa, south Europe, Australia, and south-east Asia including Timor, southern China, and the Ogasawara and Ryukyu Islands of Japan were found to belong to the southern clade, while those present in cool and temperate area in Japan and China were found to belong to the northern clade. This result was confirmed by Ma et al. (2012) who performed a more intensive analysis and reported that the northern populations of Europe belonged to the northern clade. However, the relationship between adult body size and different clades remains unknown.

To analyze the body size variation in the migratory locust, I obtained solitary adults from various localities in the Japanese Archipelago, which extends from the Ryukyu subtropical region to the Hokkaido cool-temperate region covering more than 2,500 km. As a result, the present analysis contained geographic populations differing not only in latitude but also in voltinism and origin involving the northern and southern clades (Hakomori and Tanaka 1992, H. Tanaka 1994a, b, S. Tanaka 1994, Tokuda et al. 2010). Understanding the genetic aspects of size variation is crucial, as such variation can be influenced environmentally (Stillwell 2010, Sadakiyo and Ishihara 2011). Therefore, in this study, I determined whether the body size pattern observed in field-collected locusts was due to genetic variation or environmentally induced phenotypic plasticity by comparing the body size of the progeny reared in the laboratory over three generations. The results suggest that the body size variation of the migratory locust has been influenced not only by factors such as latitude, voltinism, genetic constituents, and growing environment, such as photoperiod and phase polyphenism, but also by factors related to developmental efficiency. Additionally, I explored the implications of body size on various reproductive traits, including ovary size, egg pod size, egg number, and hatchling body size, across different local populations and latitudes.

One of the unique characteristics of certain locusts is the phase variation in body size and shape induced by crowding (Uvarov 1966, Pener 1991, Pener and Simpson 2009). For example, female adult body size tends to be larger at low population densities than at high population densities, and this difference is influenced by crowding conditions experienced during both the current and parental generations (Hunter-Jones 1958). Changes in adult body size and classical morphometric traits may take a few generations before they stabilize (Uvarov 1966). In this study, I aimed to determine whether the observed geographic variation in body size among field-collected adults was primarily influenced by genetic or environmental factors. To achieve this, locusts in different populations were reared in groups, as it was impractical to rear them in isolation while simulating field conditions. Consequently, it was essential to monitor changes in body size and classical morphometric traits over three generations. The data obtained from this study are expected to shed light on the geographic variability of locust body size and classical morphometric traits.

Sexual size dimorphism (SSD) is a common phenomenon that varies among different Orthoptera taxa (Fairbairn 1997, Whitman 2008, Bidau et al. 2016). SSD is believed to be influenced by various factors, including natural selection, sexual selection, and genetic correlations between the sexes (Whitman 2008). In the case of Caelifera species, SSD is female-biased in nearly all of the 1,106 species studied and 82% of the 390 Ensifera species (Hochkirch and Gröning 2008). However, the bushcricket *Poecilimon thessalicus* (Fischer, 1853) exhibits a male-biased SSD. Lehmann and Lehmann (2008) demonstrated that geographically different populations of this species follow Rensch's rule, with SSD decreasing as body size increases, resulting in males being relatively larger than females in populations with larger body sizes. In contrast, the migratory locust, which is also female-biased (Uvarov 1966, Farrow and Colless 1980), shows independent variations in body dimensions for each sex within a given population over different years without any significant relationship between the sexes (Tanaka 2022). In this study, I investigated the presence of Rensch's rule and variation in SSD among geographically distinct populations of the migratory locust.

The observed pattern in this insect suggests the presence of a Masaki's cline, with two major peaks in body size at the southern limits of the univoltine and bivoltine areas. This paper describes the results of these observations and discusses the geographic adaptation of the migratory locust.

## Materials and methods

*Insects.*—Adult migratory locusts were collected at different localities in the Japanese Archipelago from 2007 to 2019 (Fig. 1; Suppl. material 1: table S1). Fig. 2 illustrates the numbers of migratory locust generations per year that were inferred from the present and previous studies (A. Tanaka 1987, A. Tanaka and Kiritani 1989, H. Tanaka 1994a,b, Hakomori and Tanaka 1992, Tanaka 1994, Yamagishi and Tanaka 2009, Shimizu et al. 2012). The migratory locust is univoltine in Hokkaido and in the northern part of Honshu Island at >38.6°N. Based on the reproductive activity of field-collected individuals, Tanaka (1994) suggested that the population at Shiobara (No. 9, 36.9°N) was primarily univoltine. During the present study, both adults and nymphs were observed in early August 2008 (Suppl. material 1: fig. S1), suggesting that at least a part of the population is bivoltine. At 36.1°N (site no. 10, Fig. 1), a bivoltine life cycle is predominant (Tanaka 2022) and appears to persist until 34.2°N (site no. 14–16, Fig. 1), where both adults and nymphs were observed from July 15–17, 2008, and adults with only a few late instar nymphs were observed on October 9, 2009 (Tanaka, S.

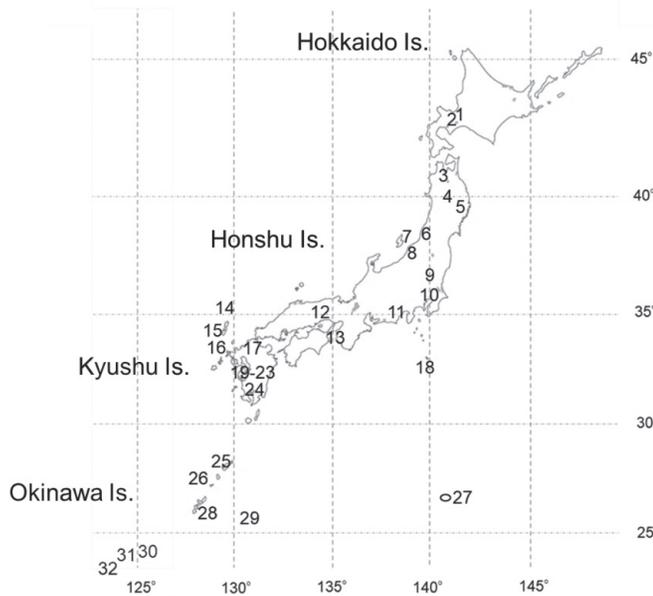


Fig. 1. Collection sites of *Locusta migratoria* in Japan. Numbers indicate the sites where locusts were collected. For the names of the sites, see Suppl. material 1: table S1.

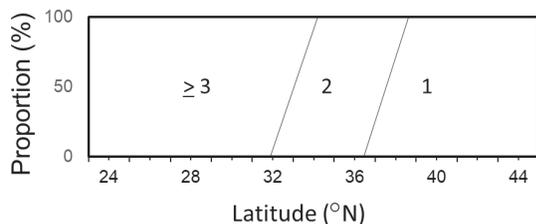


Fig. 2. Diagram showing compositions of *Locusta migratoria* populations with 1, 2 and 3 or more generations per year based on various sources (H. Tanaka 1982, Hakomori and Tanaka 1992, Tanaka 1994, Shimizu et al. 2012, Tanaka 2022).

unpublished data). South of 34.2°N, third-generation locusts appear, and at 32.1°N (site no. 23), adults from the three generations occur in June, August, and October, respectively (Shintani Y., personal communication). This locust overwinters as diapause eggs in Japan, but in the southern populations at < 30.8°N, adults also overwinter and lay eggs in February and March (A. Tanaka and Kiritani 1989, H. Tanaka 1994a, b, Tanaka 1994, Yamagishi and Tanaka 2009, Shimizu et al. 2012), suggesting that these populations consist of individuals that may produce at least 3 generations a year but overwinter at different stages depending on the time when winter is encountered. In the present study, populations located >31.5°N belonged to the north clade and those located <28.45°N belonged to the south clade, with the two clades separated by the Tokara Strait (approximately 29°N, Tokuda et al. 2010).

**Body size measurements and egg collection.**—Following the method used by Dirsh (1951, 1953) for measuring the desert locust *Schistocerca gregaria* (Forskål, 1775), the head width (C), hind femur length (F), and forewing length (E) of collected adults were measured using a digital caliper (Digipa Pro; Mitsutoyo Co., Kanagawa, Japan) to the nearest 0.1 mm. Data for the Hioki population in Kagoshima Prefecture were derived from A. Tanaka (1987). Some adults were reared individually in small nylon-screen cages (28 × 15

× 28 cm) at 30 ± 1.5°C with an LD 12:12 h photoperiod to collect egg pods. The insects were fed cut leaves and stems of *Bromus catharticus* Vahl (1791) and *Miscanthus sinensis* Andersson (1855). The egg pods were laid in moist sand (approximately 15% by weight) held in plastic cups (340 ml in volume), and the maximum diameter of each pod was measured within 3 days after deposition during which egg size showed no significant change (Tanaka and Sugahara 2017). After laying several egg pods, the adults were dissected to determine the number of ovarioles per ovary. Because most were collected during the fall generation, their eggs entered diapause. They were usually kept at 20°C for one month and then stored at 5°C for at least 3 months to terminate diapause (Tanaka 1992).

**Genetic basis for body size variation.**—Approximately 100–150 nymphs that hatched at 30°C after being chilled for diapause termination were reared in large nylon screen cages (42 × 22 × 42 cm) at 30 ± 1.5°C at LD 12:12 h and LD 16:8 h, and the duration of nymphal development was recorded. Because of the limited available space for rearing, only 1–4 cages were used for each local population. Newly emerged adults of the first laboratory generation (G1) were transferred to another cage in which they were reared for an additional 10 days or so before their body dimensions were measured as described above. Because long-day locusts often produce few eggs under crowded conditions (Verdier 1967, H. Tanaka 1982, Pener 1991, Tanaka et al. 1993, Hasegawa and Tanaka 1996, Okuda et al. 1996), eggs were collected from short-day locusts, and nymphs from the second (G2) and third laboratory generations (G3) were reared as described above to determine the duration of nymphal development and their body sizes at adult emergence.

**Measurements of reproductive traits.**—The number of ovarioles was determined by counting the ovarioles from the right ovary of dissected female adults. The value multiplied by two was used as the number of ovarioles in each individual. Preliminary observations found no significant difference in the number of ovarioles between the right and left ovarioles of females (mean ± SD = 113.8 ± 12.9 and 119.0 ± 9.7 in the right and left ovaries of a Tsuruoka population,  $t = -1.44$ , DF = 35,  $p = 0.16$ ). The maximum width of the egg pods was measured using a digital caliper under a binocular microscope. The number of eggs per pod was determined by counting hatched and dead eggs. Because locust egg length and weight increase during embryonic development (Shulov and Pener 1959, 1963, Tanaka and Sugahara 2017), hatchling body weight was measured by putting approximately 10 newly hatched nymphs (within 12 h of hatching) into a plastic tube (volume 1.5 ml) and weighing them to the nearest 0.1 mg. The mean value was used as the hatchling body weight.

**Air temperature.**—Annual mean temperatures over a maximum of 20 years at or near the collection sites were obtained from the Japan Meteorological Agency (2018). The temperatures at high altitudes were corrected by assuming that the temperature changed by 0.6°C every 100 m.

**Statistical methods.**—The relationships between locust body sizes and the latitudes, longitudes, and altitudes of the collection sites were analyzed using Pearson correlation coefficients, except for a few cases in which a quadratic equation gave a higher  $R^2$  value than a linear equation. Body sizes were compared using a  $t$ -test and Tukey's multiple comparison test. Morphometric ratios and ratios of male to female body sizes were analyzed using the Mann Whitney's  $U$  test and the Steel-Dwass test. These analyses were performed using a statistics service available at <http://www.gen-info>.

osaka-u.ac.jp/MEPHAS/kaiseki.html, Descriptive Statistics (Excel, Microsoft Office 365) or StatView (SAS Institute Inc., NC, USA). The differences were judged as significant when  $p < 0.05$ .

## Results

*Correlations between latitudes, longitudes, altitudes, and annual mean air temperatures at the collection sites.*—The latitudes of the collection sites showed a significant correlation with longitudes but not with altitudes (Table 1). These three variables were significantly correlated with the annual mean temperatures ( $p < 0.01$  each) and the latitude showed the highest correlation coefficient ( $r = -0.95$ ).

**Table 1.** Correlations between latitudes (LAT), longitudes (LON), altitudes (ALT) and annual mean temperatures (AMT) of the collection sites.

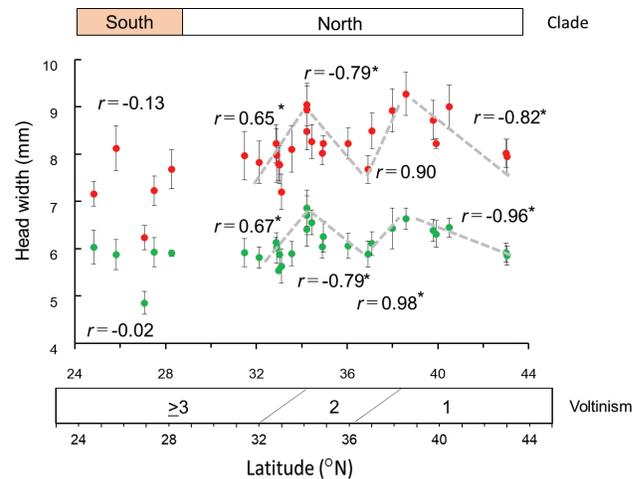
Variables	N	<i>r</i>	<i>R</i> <sup>2</sup>	<i>p</i>
LAT versus LON	31	0.74	0.56	<0.001
LAT versus ALT	31	0.30	0.09	0.106
LON versus ALT	31	0.22	0.05	0.234
LAT versus AMT	31	-0.95	0.91	<0.001
LON versus AMT	31	-0.67	0.45	<0.001
ALT versus AMT	31	-0.56	0.32	<0.001

Bold letters indicate  $p < 0.05$ .

Data are based on Suppl. material 1: table S1.

*Latitudinal variation in body size.*—Adult head widths of field-collected migratory locusts were plotted against latitudes (Fig. 3). The sample sizes are given in Suppl. material 1: table S2. In both sexes, a significant positive overall correlation was observed between the two variables. However, the correlation was not as high: the *r* and *R*<sup>2</sup> were 0.57 and 0.32 in females ( $p < 0.05$ ;  $N = 29$ ) and 0.44 and 0.19 in males ( $p < 0.05$ ;  $N = 29$ ). A regression analysis indicated that the slope was steeper in females (0.077, *R*<sup>2</sup> = 0.32) than in males (0.039, *R*<sup>2</sup> = 0.19). When the values for the north and south clade populations were analyzed separately, no significant correlation was observed in either the north ( $r = 0.32$ ,  $N = 24$ ,  $p = 0.12$  in females;  $r = 0.17$ ,  $N = 24$ ,  $p = 0.42$  in males) or south clade ( $r = -0.06$ ,  $N = 5$ ,  $p = 0.93$  in females;  $r = -0.20$ ,  $N = 5$ ,  $p = 0.77$  in males). Although the sample size for the south clade populations was small ( $N = 5$ ), their mean head width (mean  $\pm$  SD =  $7.32 \pm 0.70$  and  $5.65 \pm 0.46$  in females and males) was smaller than that of the north clade populations ( $N = 24$ , mean  $\pm$  SD =  $8.26 \pm 0.51$  and  $6.16 \pm 0.36$  in females and males), and the difference between the two clades was significant in females ( $t = 2.82$ ,  $DF = 5$ ,  $p < 0.05$ ) or marginally significant in males ( $t = 2.23$ ,  $DF = 5$ ,  $p = 0.068$ ), suggesting that the positive correlations observed above might be related to phylogenetic differences.

The variation in head widths illustrated in Fig. 3 appears to show a saw-toothed pattern related to voltinism. Significant correlations between the head widths and latitudes were observed when the data were calculated for different ranges with respect to voltinism (Fig. 3). Within the zone of univoltine life cycles (43.1–38.6°N), the width tended to increase toward the south in both sexes ( $p < 0.05$ , Suppl. material 1: table S3). This tendency was reversed in the transitional zone of the univoltine and bivoltine life cycles (38.6–36.9°N;  $p < 0.05$ ), although the correlation was insignificant in females likely due to the small sample size. In the bivoltine zone (36.9–34.2°N), head width again showed an increasing tendency toward the south ( $p < 0.05$ ). Then, the tendency was reversed again in the transitional zone of the bivoltine and trivoltine life cycles (34.2–31.5°N;  $p < 0.05$ ). In the southernmost zone with a trivoltine life cycle (31.5–24.8°N), no significant correlation was observed in either sex ( $p > 0.05$ ).

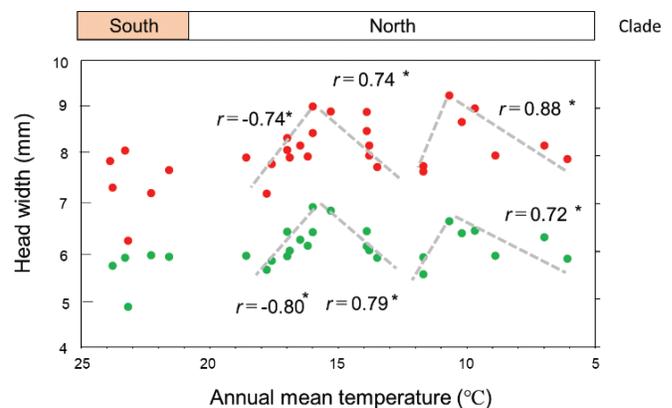


**Fig. 3.** Geographic variation in head widths (mean  $\pm$  SD) of *Locusta migratoria* adults collected at various latitudes. Top and bottom diagrams illustrate the phylogenetic origin (Tokuda et al. 2010) and number of generations per year (as shown in Fig. 2). Red and green symbols indicate females and males, respectively. *r* indicates the correlation coefficient within each zone (see Suppl. material 1: table S3). \*,  $p < 0.05$ ; \*\*,  $p < 0.01$ . Data are based on Suppl. material 1: table S2.

A saw-toothed pattern was also observed when the head widths were plotted against the annual mean temperatures of the collection sites (Fig. 4). In contrast, the two variables showed no significant correlation within the north clade range in either females ( $r = -0.18$ ,  $N = 24$ ,  $p = 0.42$ ) or males ( $r = 0.02$ ,  $N = 24$ ,  $p = 0.93$ ).

*Longitudinal and altitudinal variations in body size.*—Head width showed no significant correlation with either the longitudes or altitudes of the collection sites (Fig. 5).

*Genetic basis of body size variation.*—To determine whether the saw-toothed pattern observed in field-collected locusts was formed by their genetic variation or phenotypic plasticity, their offspring were reared in the laboratory for three generations, and various body parameters were measured (Suppl. material 1: table S4). The pat-



**Fig. 4.** Head widths (mean  $\pm$  SD) of field-collected *Locusta migratoria* adults plotted against the annual mean temperatures at the collection sites. Top diagrams show the phylogenetic origin (Tokuda et al. 2010) and number of generations per year (as shown in Fig. 2). Red and green symbols indicate females and males, respectively. Data are based on Suppl. material 1: table S2.

terns of changes in head widths over the latitudinal range looked similar at the two tested photoperiods (Fig. 6), but the head width at LD 16:8 h was significantly larger in both sexes than that at LD 12:12 h in all laboratory generations ( $t$ -test,  $p < 0.05$ ) except for G2 males with a marginally significant difference (Table 2A).

In G1, a saw-toothed pattern was obvious in head widths plotted against latitudes, with two peaks occurring at 38.6 and 34.2°N (Fig. 6A, B), similar to the pattern observed for the field-collected individuals shown in Fig. 3. At LD 12:12 h, head widths of females and males significantly increased southward in the univoltine zone (43.1–38.6°N), decreased southward in the transitional zone of the uni- and bivoltine zones (38.6–36.9°N), increased again in the bivoltine zone (36.9–34.2°N) and declined gradually in the transitional zone of the bi- and trivoltine zones (34.2–31.5°N; Suppl. material 1: table S4A). In the south clade at  $< 28.5^\circ\text{N}$ , head widths significantly increased southward in males but not in females (Suppl. material 1: table S4A). Similar geographical patterns of variation were observed at LD 16:8 h in G1 and at the two photoperiods in G2 and G3 (Fig. 6B–F), although statistical

**Table 2.** Comparison of head widths of *Locusta migratoria* collected at different localities (G0) and reared at LD 12:12 h and LD 16:8 h for 3 generations (G1–3). (A) Differences in head width at LD 12:12 h and LD 16:8 h. (B) Effect of generation on adult head width.

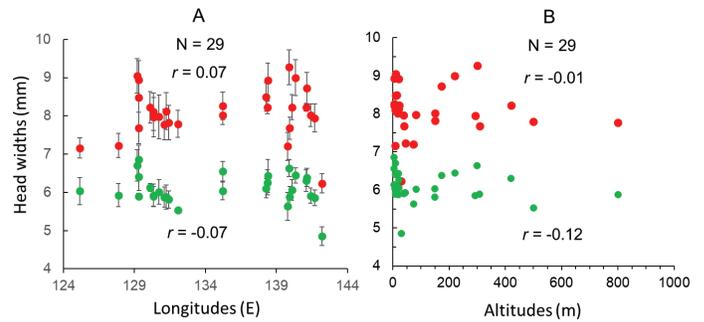
(A)					
Generations	$t$ value	DF	$p$		
G1 females	-2.59	46	<b>&lt;0.05</b>		
G1 males	-3.23	45	<b>&lt;0.05</b>		
G2 females	-2.01	49	<b>&lt;0.05</b>		
G2 males	-1.96	49	0.055		
G3 females	-2.01	30	<b>&lt;0.05</b>		
G3 males	-1.96	28	<b>&lt;0.05</b>		
(B)					
Photoperiod	Generations	N	Mean, mm	SD, mm	Tukey's multiple test
Females					
	0	29	8.10	0.65	a
LD 12: 12h	1	60	7.64	0.38	b
LD 12: 12h	2	27	7.64	0.39	b
LD 12: 12h	3	26	7.61	0.30	b
Males					
	0	29	6.07	0.42	a
LD 12: 12h	1	60	6.46	0.31	b
LD 12: 12h	2	27	6.48	0.31	b
LD 12: 12h	3	26	6.43	0.36	b
Females					
	0	29	8.10	0.64	–
LD 16: 8h	1	31	7.92	0.53	–
LD 16: 8h	2	24	7.85	0.37	–
LD 16: 8h	3	19	7.85	0.45	–
Males					
	0	29	6.07	0.42	a
LD 16: 8h	1	31	6.75	0.46	b
LD 16: 8h	2	24	6.65	0.30	b
LD 16: 8h	3	19	6.73	0.40	b

Bold characters indicate  $p < 0.05$ .

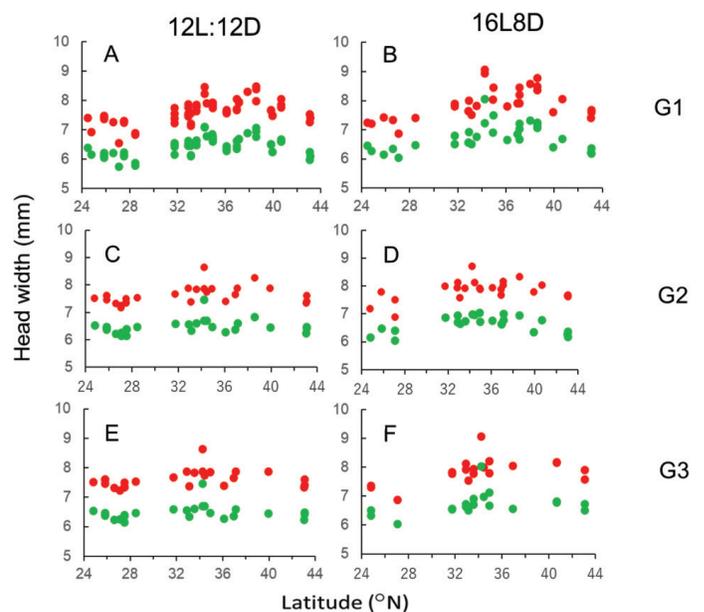
N indicates the number of adults collected at different localities (G0) or the number of cages in G1–G3.

Letters in sex and photoperiod columns indicate significant differences in mean values at  $p < 0.05$  using Tukey's multiple test.

Dash indicates ANOVA ( $p = 0.27$ ,  $DF = 3$ , 99) showed no significant difference among generations.



**Fig. 5.** Mean head widths of field-collected *Locusta migratoria* adults plotted against the longitudes (A) and altitudes (m) of the collection sites. Red and green symbols indicate females and males, respectively. SDs expressed as bars are given only in (B). None of the correlations are statistically significant ( $p > 0.05$ ). Data are based on Suppl. material 1: tables S1, S2.



**Fig. 6.** Geographic variation in head widths of *Locusta migratoria* adults reared at LD 12:12 h or LD 16:8 h (30°C) in the first 3 laboratory generations. Red and green symbols showing means per cage indicate females and males, respectively. Data are based on Suppl. material 1: table S3.

significance was not attained in some zones likely due to the small sample sizes and lack of data points from the southern area of the univoltine zone (Suppl. material 1: table S4B). These results suggest that the saw-toothed pattern observed in field-collected individuals is related to the geographical variation in the genetic constituents of the locusts.

Compared with G0, mean head width was significantly decreased in females and increased in males at G1 that were reared at LD 12:12 h, while no further significant change was observed in G2 and G3 (Table 2B). At LD 16:8 h, a similar tendency was observed in males but not in females (ANOVA,  $p = 0.773$ ,  $DF = 3$ , 99, Table 2B).

**Geographic variation in reproductive traits.**—The maximum widths of egg pods laid by G0 females were significantly correlated with latitudes of the original habitats ( $R^2 = 0.50$ ;  $N = 28$ ;  $p < 0.0001$ ; Fig. 7A, Suppl. material 1: table S5). However, closer examination found

that the egg-pod widths were relatively small in the south clade populations and tended to increase with latitudes in the north clade populations until  $38.6^{\circ}\text{N}$  ( $R^2 = 0.75$ ;  $N = 23$ ;  $p < 0.0001$ ). At around  $> 38.6^{\circ}\text{N}$ , the values appeared to decrease as the latitude increased, although the negative correlation was insignificant ( $r = -0.56$ ,  $R^2 = 0.31$ ;  $N = 6$ ,  $p = 0.19$ ). The pattern observed here was different from that observed in adult body or head size, as shown in Fig. 3. Although no attempt was made to measure the amount of accessory gland material covering the eggs, it was easy to distinguish the egg pods produced by the two clades because the layer covering eggs was thinner in the south-clade populations than in the north-clade ones.

A similar latitudinal pattern was observed in the numbers of eggs per egg pod, which showed a significant correlation coefficient of 0.63 ( $N = 26$ ,  $p < 0.001$ , Fig. 7B). The correlation was increased when calculated at around  $< 38.6^{\circ}\text{N}$  ( $r = 0.75$ ,  $N = 21$ ,  $p < 0.0001$ ). In all the north-clade populations, however, the correlation was not significant ( $r = -0.08$ ,  $N = 19$ ,  $p = 0.73$ ). In the south-clade populations, a negative correlation was observed, although the sample size was small ( $r = -0.88$ ,  $N = 7$ ,  $p < 0.01$ ).

No significant correlation was observed between egg-pod width and number of eggs per pod in either north- (Fig. 8A,  $r = 0.46$ ,  $N = 19$ ,  $p = 0.15$ ) or south-clade populations ( $r = 0.60$ ,  $N = 5$ ,  $p = 0.33$ ), although the combined data showed a significant correlation ( $r = 0.80$ ,  $R^2 = 0.65$ ,  $N = 24$ ,  $p < 0.001$ ). Both the number of eggs per pod ( $r = 0.61$ ,  $R^2 = 0.37$ ,  $N = 28$ ,  $p < 0.0001$ , Suppl. material 1: table S5) and egg-pod width ( $r = 0.76$ ,  $R^2 = 0.58$ ,  $N = 26$ ,  $p < 0.0001$ ) were significantly correlated with the head width of female adults. Within the north clade, however, head widths were significantly correlated only with the former (Fig. 8B, C). In the south clade, the sample sizes seemed too small to display any reliable trend.

The number of ovarioles from female adults also showed large variations, as shown for G0 and G1 in Fig. 9A and Suppl. material 1: table S6 in which the data from the two photoperiods were combined for G1 because no significant difference was observed in the overall mean values between the two photoperiods ( $p > 0.05$ , Suppl. material 1: table S7). Relatively large numbers of ovarioles were observed in a range between  $36$  and  $38^{\circ}\text{N}$  and the quadratic equation gave the highest  $R^2$  values, with  $0.82$  ( $p < 0.01$ ,  $N = 21$ ) and  $0.70$  ( $p < 0.0001$ ,  $N = 34$ ) in G0 and G1, respectively; Fig. 9A). The number of ovarioles in the G2 females did not show a significant correlation with latitude ( $r = 0.51$ ;  $R^2 = 0.25$ ;  $N = 23$ ;  $p = 0.056$ ). The mean number of ovarioles was not significantly different between G0 and G1 but was reduced in G2 (Fig. 9B, Tukey's multiple test,  $p < 0.05$ ). A significant correlation was observed between the number of ovarioles and head widths of female adults in the respective generations ( $r = 0.65$ ,  $0.54$ , and  $0.55$  in G0, G1, and G2, respectively,  $p < 0.01$  each) as

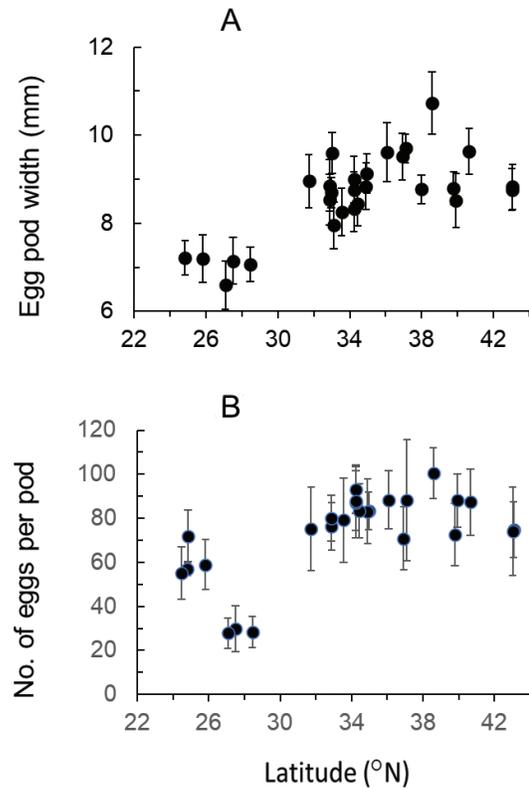


Fig. 7. Means and SDs of maximum egg pod widths (A) and numbers of eggs (B) of egg pods produced by field-collected *Locusta migratoria* plotted against the latitudes of collection sites. Data are based on Suppl. material 1: table S5.

well as in the 3 generations combined ( $y$  (no. of ovarioles) =  $12.77 \times$  (head width, mm) +  $10.54$ ;  $r = 0.59$ ,  $R^2 = 0.35$ ;  $N = 77$ ,  $p < 0.001$ , Fig. 9C). A highly significant correlation was observed between the number of ovarioles and that of eggs per pod ( $r = 0.82$ ,  $N = 20$ ,  $p < 0.0001$ ;  $y$  (no. of eggs) =  $1.70 \times$  (no. of ovarioles) -  $123.57$ ,  $R^2 = 0.67$  based on the data in Suppl. material 1: tables S5, S6).

The proportion of functional ovarioles was determined for G0 based on the mean number of eggs per pod and that of ovarioles in each population (Fig. 9D, Suppl. material 1: tables S5, S6), which showed a significant correlation with latitude ( $r = 0.58$ ;  $N = 20$ ;  $p < 0.01$ ), but no significant correlation was observed either among the north- ( $r = -0.01$ ;  $N = 16$ ;  $p = 0.97$ ) or south-clade populations ( $r = -0.86$ ;  $N = 4$ ;  $p = 0.20$ ). The mean proportion of functional ovarioles was  $62.8\%$  ( $N = 470$ ).

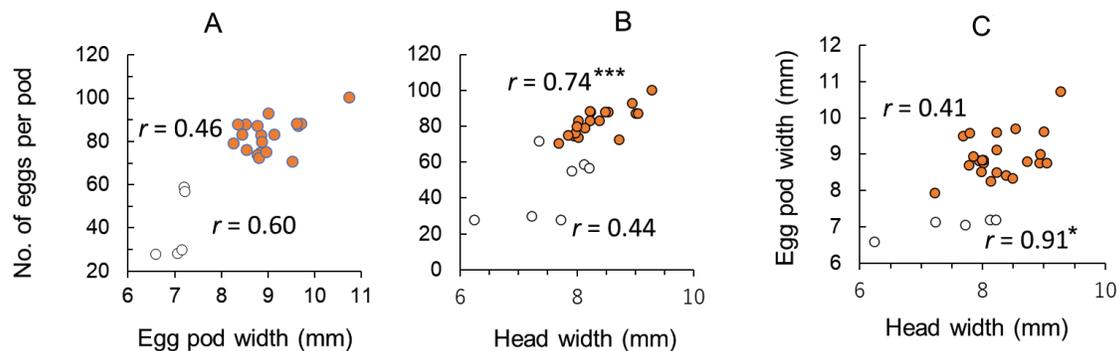
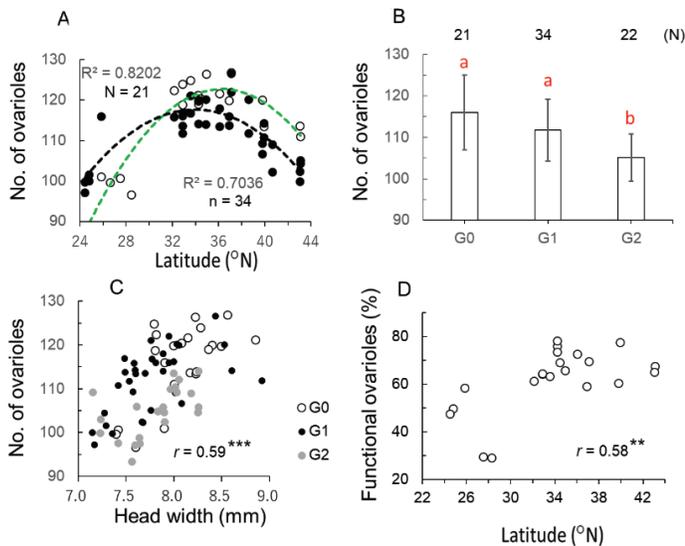
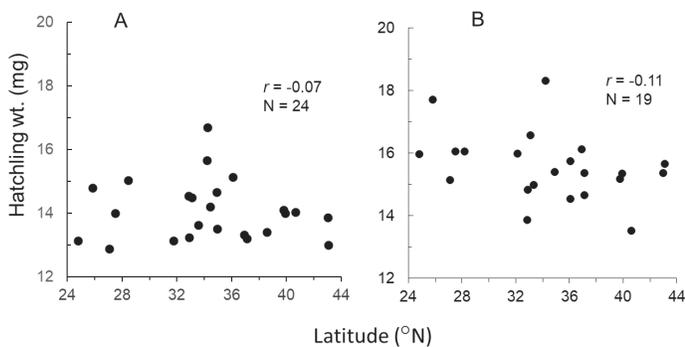


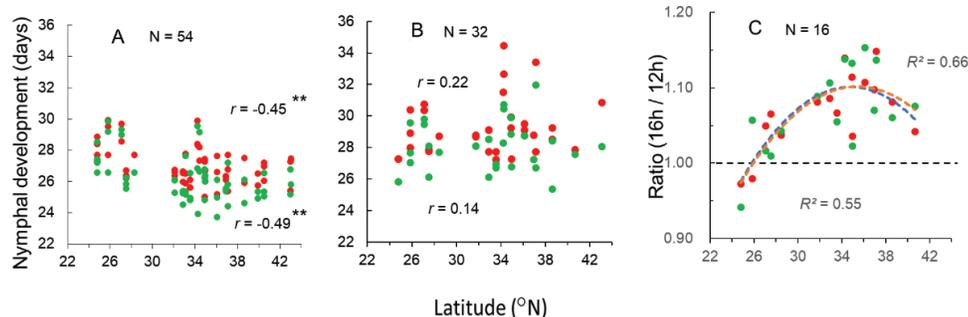
Fig. 8. Relationships between numbers of eggs per pod, egg pod widths, and head widths of *Locusta migratoria* female parents collected in the field. \*,  $p < 0.05$ ; \*\*\*,  $p < 0.001$ . Orange and white symbols indicate populations of the north and south clades, respectively. Data are based on Suppl. material 1: table S5.



**Fig. 9.** Numbers of ovarioles in field-collected and lab-reared *Locusta migratoria* females plotted against the latitudes (A), generations (B), and head widths of females of the parental generation, (C) and the proportions of functional ovarioles (no. of eggs / no. of ovarioles) plotted against the latitudes in field-collected females (D). \*\*,  $p < 0.01$ ; \*\*\*,  $p < 0.001$ . G0, field-collected generation; G1, 1<sup>st</sup> lab-reared generation; G2, 2<sup>nd</sup> lab-reared generation. Mean numbers of ovarioles ( $\pm$  SD) among generations in (B) are compared with the Tukey's multiple comparison test. Different letters indicate significant differences at the 5% level. Data are based on Suppl. material 1: table S6.



**Fig. 10.** Body weight of hatchlings from eggs laid by G0 and G1 *Locusta migratoria* females. Each N is based on 51–443 hatchlings (mean = 190.8). N indicates the number of populations (see Suppl. material 1: table S8). Correlations are insignificant at the 5% level.



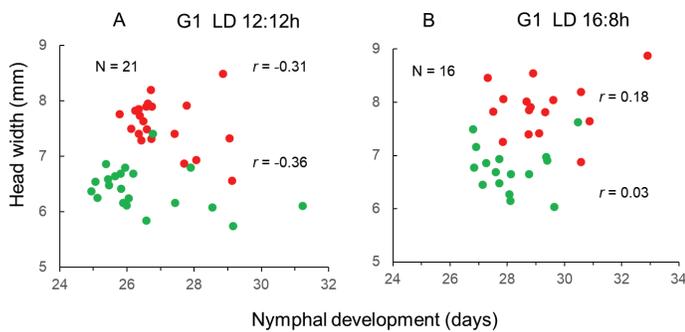
**Fig. 11.** Nymphal development in G1 *Locusta migratoria* reared at LD 12:12 h (A) and LD 16:8 h (B) and the ratios of nymphal development at LD 16:8h to that at LD 12:12 h (C) plotted against the latitudes. Red and green symbols indicate females and males, respectively. N indicates sample size based on Suppl. material 1: table S9. \*\*,  $p < 0.01$ .

The body weight of hatchlings from eggs laid by G0 females from 24 different populations was 14.1 mg (SD = 0.9 mg) on average and showed no significant correlation with the latitude of the collection sites ( $p = 0.75$ ,  $N = 24$ , Fig. 10A and Suppl. material 1: table S8). Body weight was significantly increased in the hatchlings produced by G1 females (mean  $\pm$  SD = 15.7 mg  $\pm$  1.1 mg,  $N = 19$ ,  $t = -4.96$ ,  $DF = 35$ ;  $p < 0.001$ ) but showed no significant correlation with latitude ( $p = -0.11$ ,  $N = 19$ , Fig. 10B). Hatchling body weight was not significantly correlated with head width of the female parent either in the progeny of G0 ( $r = 0.36$ ,  $N = 23$ ,  $p = 0.09$ ) or in those of G1 ( $r = 0.004$ ,  $N = 19$ ,  $p = 0.99$ ).

**Nymphal development and adult body size.**—When the mean duration of nymphal development per cage between the two photoperiods in G1 was compared, it was significantly shorter at LD 12:12 h than at LD 16:8 h: mean  $\pm$  SD = 27.1  $\pm$  1.2 days vs. 29.3  $\pm$  1.8 days in females ( $t = -6.00$ ,  $DF = 49$ ,  $p < 0.0001$ ); 26.3  $\pm$  1.5 days vs. 28.1  $\pm$  1.6 days in males ( $t = -5.26$ ,  $DF = 64$ ,  $p < 0.0001$ , Suppl. material 1: table S9A). Thus, the data obtained during the two photoperiods were analyzed separately. The duration of nymphal development showed a significant negative correlation with latitude at LD 12:12 h (Fig. 11A). In each clade, however, no significant correlation was observed between the two variables ( $p > 0.05$ , Suppl. material 1: table S9B). At LD 16:8 h, the two variables showed no significant correlation ( $p > 0.05$ , Fig. 11B). Relative lengths of nymphal development at LD 16:8 h to that at LD 12:12 h tended to be prolonged in the bivoltine populations in the range of 34 to 37°N, and the photoperiodic effect on nymphal development became less obvious toward the northern and southernmost populations (Fig. 11C, Suppl. material 1: table S9C).

No significant correlation was observed between the length of nymphal development and adult head width at either LD 12:12 h (Fig. 12,  $r = -0.31$ ,  $N = 21$ ,  $p = 0.176$  in females;  $r = -0.30$ ,  $N = 21$ ,  $p = 0.111$  in males) or at LD 16:8 h ( $r = 0.18$ ,  $N = 16$ ,  $p = 0.518$  in females;  $r = 0.03$ ,  $N = 16$ ,  $p = 0.929$  in males). This result suggests that the saw-toothed pattern observed in this locust (Figs 3, 4, 6) is not a direct reflection of the variable duration of nymphal development.

**Growth efficiency and adult body size.**—The growth efficiency, calculated as the head width (mm) divided by the duration of nymphal development (days), in G1 was found to be high in the bivoltine area and low in both the northern and southern regions of this area (Fig. 13A). Moreover, there was a strong positive correlation between growth efficiency in G1 and the head widths of G0 adults, particularly when the values obtained under LD 12:12 h conditions were considered (Fig. 13B, C, Suppl. material 1: table S10), suggesting that the progeny from larger field-collected adults tended to exhibit higher growth efficiency.



**Fig. 12.** Relationships between lengths of nymphal development and adult head width in G1 *Locusta migratoria* reared at LD12:12 h (A) and LD 16:8 h (B). Correlations are insignificant at the 5% level. Red and green symbols indicate females and males, respectively. Each symbol indicates the mean of each population based on Suppl. material 1: table S10.

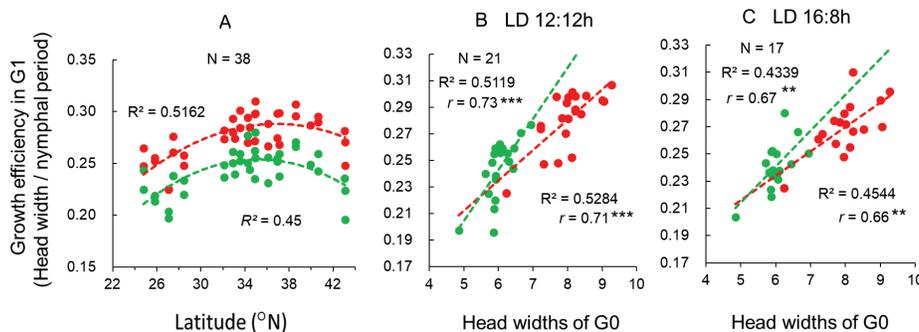
**Phase-related variation.**—The F/C showed a significant negative correlation with latitude in both sexes in G0 (Fig. 14A). At LD 12:12 h, this tendency was consistent in G1–G3 (Fig. 14B–D), which were reared under crowded conditions. However, among the north-clade populations, a significant correlation was observed only in females of G0 and G1 ( $r = -0.54$ ,  $p < 0.001$ , Suppl. material 1: table

S11A, B). The F/C was significantly larger in the south clade than in the north clade in all generations including G0 (Suppl. material 1: table S11C), suggesting the presence of a possible phylogenetic difference. The males had larger F/C values than the females in all generations (Fig. 14, Suppl. material 1: table S11D). Similar results were observed at LD 16:8 h (Suppl. material 1: fig. S2, table S11).

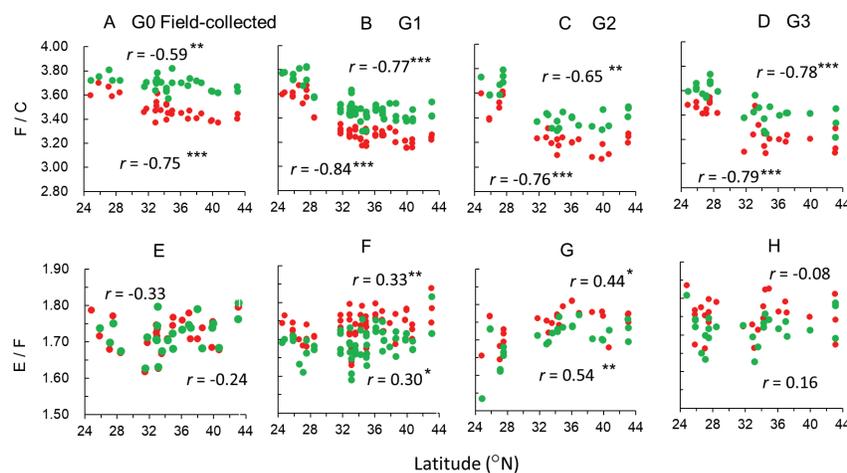
The correlation between E/F values and latitudes was insignificant in G0 and G3 (Fig. 14E, H), while it was significant in G1 and G2 (Fig. 14F, G, Suppl. material 1: tables S2, S11). Within each clade, it was significant in G0 and G1 and insignificant in G2 and G3 (Suppl. material 1: table S11B). The E/F was similar between the two clades in all generations except for G2 at LD 12:12 h (Suppl. material 1: table S11C). Males had consistently smaller E/F values than females ( $p < 0.05$ , Suppl. material 1: table S11D).

Compared with the values for G0, F/C significantly decreased in G1 in both sexes at both photoperiods, and no further change was observed in G2 and G3 (Fig. 15A, B), whereas the E/F showed no significant change at both photoperiods except for G1 at LD 12:12 h (Fig. 15C, D).

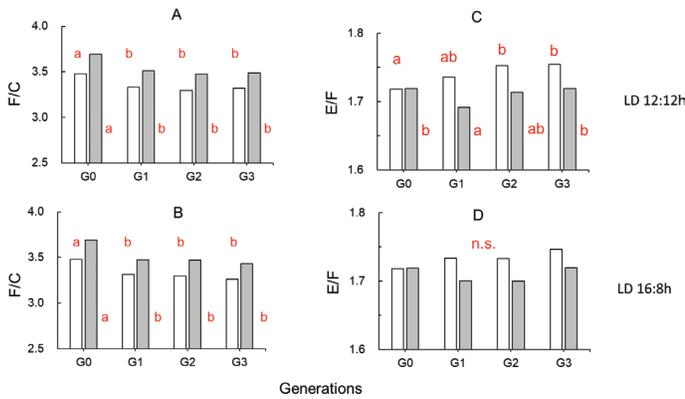
**Sexual size dimorphism (SDD) in the field and laboratory.**—Field-collected male and female head widths were highly correlated with each other when the mean values of different local populations were analyzed ( $y$  (male head width, mm) =  $0.59 \times$  (female



**Fig. 13.** The growth efficiencies, as determined by adult head width/duration of nymphal development, plotted against the latitudes (A) and correlation between adult head widths of G0 and growth efficiencies of G1 at LD 12:12 h (B) or LD 16:8 h (C) in *Locusta migratoria*. N indicates sample sizes. \*\*,  $p < 0.01$ ; \*\*\*,  $p < 0.0001$ . Red and green symbols indicate females and males, respectively. In (A) the quadrat equation is  $y = -0.0003x^2 + 0.0248x - 0.1684$  in females and  $y = -0.0003x^2 + 0.0248x - 0.1684$  in males. Data are based on Suppl. material 1: tables S9, S10.



**Fig. 14.** F/C (hind femur length / head width) and E/F (forewing length/hind femur length) ratios of *Locusta migratoria* adults collected in the field (G0) and those reared at LD 12:12 h (G1–G3). Red and green symbols indicate females and males, respectively. Symbols in (A) and (E) indicate the mean of each population and those in (B–D, F–H) indicate the mean of individuals per cage. Data are based on Suppl. material 1: tables S2, S3. \*,  $p < 0.05$ ; \*\*,  $p < 0.01$ ; \*\*\*,  $p < 0.0001$ .



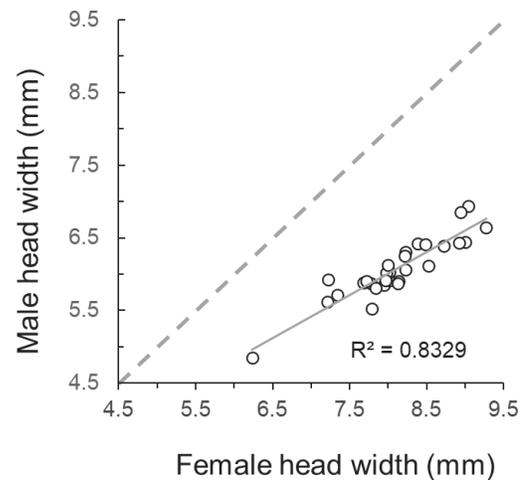
**Fig. 15.** Changes in mean F/C (hind femur length/head width) and E/F (forewing length/hind femur length) ratios of adults across generations in *Locusta migratoria*. Sample sizes in G0–3 are 29, 30, 27 and 26 in (A) and (C) and 29, 31, 24 and 19 in (B) and (D). Locusts were reared in a group in G1–G3 at 30 °C under LD12:12h or LD 16:8h. White and gray histograms indicate females and males, respectively. Different letters indicate significant differences in mean values with the Steel-Dwass test ( $p < 0.05$ ). Data are based on Suppl. material 1: tables S2, S3.

head width, mm) – 1.28,  $R^2 = 0.83$ ,  $N = 29$ ,  $p < 0.001$ , Fig. 16). An analysis of log-transformed data showed a relative decrease in male head width compared to female head width ( $y$  (male head width, mm) =  $0.78 \times$  (female head width, mm) + 0.07,  $R^2 = 0.84$ ,  $N = 29$ ,  $p < 0.001$ ; Suppl. material 1: fig. S3A), suggesting that SSD increased as female body size increased. Similar results were obtained in G1–G3 (Suppl. material 1: fig. S3B–D).

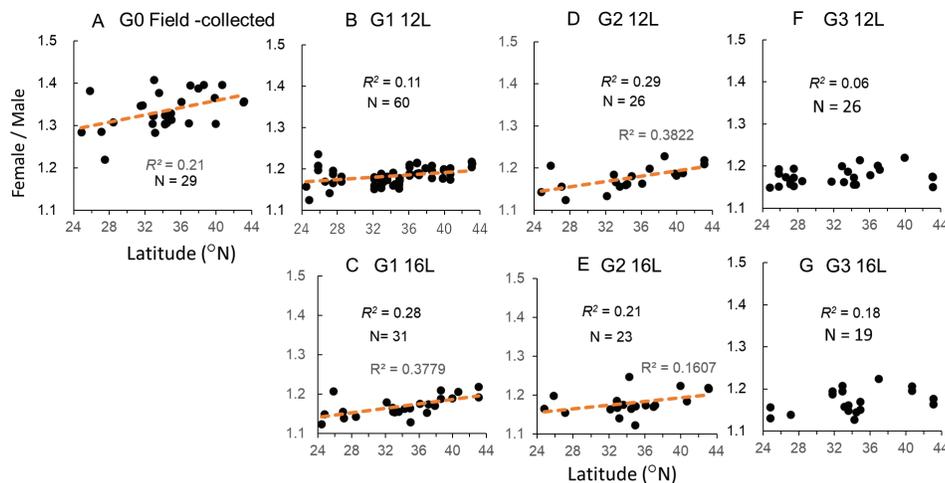
The ratios of female head widths to male head widths tended to increase with latitude in G0 ( $r = 0.46$ ,  $R^2 = 0.21$ ,  $N = 29$ ,  $p < 0.05$ , Fig. 17A, Suppl. material 1: table S12), suggesting that SSD increased with latitude. This tendency was maintained in G1–G3, and the correlations between the two variables were significant in G1 and G2 at both photoperiods ( $p < 0.05$ ) but not in G3 (Fig. 17B–G, Suppl. material 1: table S12). The mean ratios were greatly reduced from G0 (mean = 1.34,  $N = 29$ ) to G1 (mean = 1.18,  $N = 60$ , Steel-Dwass test,  $p < 0.05$ ), but no further significant change was observed in G2 (mean = 1.18,  $N = 26$ , Steel-Dwass test,  $p > 0.05$ ) or G3 (mean = 1.18,  $N = 26$ , Steel-Dwass test,  $p > 0.05$ ).

## Discussion

**Geographic clines.**—The present study demonstrated that the migratory locusts collected in the Japanese Archipelago exhibited large variations in body size and related traits. Body size and head width were significantly correlated with latitude and annual mean temperature of the collection sites but not with longitude and altitude. The latitude and annual mean temperature of the collection sites were highly correlated with one another (Table 1). Upon close examination, it became evident that the latitudinal variations in body size among the migratory locust populations were complex, exhibiting a saw-toothed pattern reminiscent of Masaki's cline, initially described for two species of ground cricket, *D. nigrofasciatus* and *P. mikado* (Masaki 1973, 1978a, 1996, Matsuda et al. 2018). Unlike the crickets, which produce 1 or 2 generations per year, the migratory locust studied here produces 1–3 generations depending on the latitude. In the univoltine area, body size tended to increase southward and rapidly decreased in the transitional area from the univoltine to bivoltine life cycles. Body size again increased south-



**Fig. 16.** Relationships between male and female head widths of field-collected *Locusta migratoria* adults. The dashed line indicates similar body sizes of both sexes. Data are based on Suppl. material 1: table S2.



**Fig. 17.** Ratios of female head width to male head width of *Locusta migratoria* adults plotted against the latitudes in the field-collected adults (G0) and those reared at LD 12:12 h (B, D, F) and LD 16:8 h (C, E, G). The correlations between the two variables are all significant ( $p < 0.05$ ) except for G3. Data are based on Suppl. material 1: tables S2, S3.

ward in the bivoltine area and then decreased in the transient area where bi- and trivoltine life cycles occurred. In the subtropical range where the life cycle is primarily trivoltine (Yamagishi and Tanaka 2009, Shimizu et al. 2012), no significant pattern was observed.

The control of voltinism in the migratory locust is well understood. Embryonic diapause plays a key role in controlling seasonal life cycles or voltinism (Verdier 1969, 1971, 1972, Hakomori and Tanaka 1992, Tanaka 1992, 1994, H. Tanaka 1994a, b, Tanaka and Zhu 2008, Yamagishi and Tanaka 2009). In univoltine populations, the majority of eggs enter diapause regardless of parental photoperiod. In bivoltine populations, the induction of diapause depends on the parental photoperiod during adult life and embryonic temperature. Diapause is induced when parents are exposed to short days and the eggs are incubated at moderately low temperatures. These conditions prevail in the fall. In contrast, eggs laid early in the summer hatch without entering diapause because parents experience long daylengths and eggs are exposed to high temperatures. In trivoltine populations, the eggs produced by the first two generations hatch without diapause in the summer, whereas those laid by the third generation in the fall enter diapause in response to short daylengths and moderately low temperatures. The south-clade populations in the Ryukyu Islands also produce three generations (Shimizu et al. 2012). However, under mild winter conditions, they overwinter at any developmental stage, including eggs, nymphs, and adults (Yamagishi and Tanaka 2009, Shimizu et al. 2012). In these populations, incubation temperature is more important for inducing diapause than the parental photoperiod (H. Tanaka 1994a, Yamagishi and Tanaka 2009), as also observed in a subtropical Hainan population in China (19.2°N, 109.4°E, Tanaka and Zhu 2008).

In the saw-toothed pattern of body size in the migratory locust, body size decreased when the number of generations per year increased from 1 to 2 and from 2 to 3. Within the univoltine or bivoltine area, body size tended to increase with a longer growing season, similar to the converse Bergmann pattern observed in many univoltine insects (Masaki 1967, 1996, Tanaka 1991, Bidau et al. 2016). This phenomenon appears to have clear adaptive significance, as the larger body size observed during a longer growing season is associated with greater fecundity. However, unlike crickets (Masaki 1967, 1978a), this locust showed a relatively small variation in nymphal development both within and among populations; the maximum relative ratio of nymphal development at a short photoperiod relative to that at a long photoperiod was less than 1.2 (Fig. 11C), whereas it was approximately 2 in crickets (Masaki 1978a, 1979). Consequently, unlike the crickets (Masaki 1967, 1978a), the body size of this locust does not show a significant correlation with nymphal development, as demonstrated in this study.

In contrast, growth efficiency, as determined by body size/nymphal development in the laboratory, showed a positive correlation with latitude in both sexes and exhibited a high correlation with the body size of field-collected adults. The higher correlation coefficients observed under LD 12:12 h than under LD 16:8 h might be related to the fact that G0 adults in multivoltine populations were 2<sup>nd</sup> or 3<sup>rd</sup> generations that had grown under medium to short daylengths.

In the transitional area from univoltine to bivoltine life cycles, the two species of crickets use variable lengths of nymphal development in response to daylengths to adjust the times of adult emergence and the deposition of diapause eggs (Masaki 1972, 1978b). How does the migratory locust solve this problem? Migratory locusts also use daylengths to control the timing of oviposition, but they modify the preoviposition period in a unique way (Tanaka et al. 1993). Locusts do not reproduce immediately after adult emergence but require a few weeks to start laying eggs (Uvarov 1966).

In the laboratory, they are often reared in groups, and their sexual maturation is strongly suppressed under a long photoperiod (Verdier 1967, Perez et al. 1971, Poras et al. 1983, Pener 1991, H. Tanaka 1994a, b, Hasegawa and Tanaka 1996, Okuda et al. 1996, Li et al. 1998). However, under semi-natural conditions, group-reared locusts started laying eggs rapidly even under long-day conditions, probably because they have experienced fluctuating temperatures (Hasegawa and Tanaka 1996). This locust apparently responds to daylengths differently depending on the phase or crowding conditions (Hasegawa and Tanaka 1996). In central Japan (site no. 10), solitary female adults emerging in August required 250–350 day-degrees to start oviposition, and those emerging in September required less, ranging from 250 to < 200 day-degrees. However, these values were not fixed and were greatly reduced in a different year when the weather was unusually cool (Tanaka et al. 1993). These responses likely serve as a mechanism to facilitate timely deposition of diapause eggs in a seasonally and annually changing environment in the transitional zones. Although little information is available about the environmental control of the preoviposition period in other solitary populations, this trait varies greatly depending on various factors—particularly daylength, temperature, and phase during the nymphal and adult stages and may represent a substantial portion of the generation time.

Much of the variation in the body size of field-collected migratory locusts appears to be due to genetic variation in local populations rather than to phenotypic plasticity, as a similar geographic pattern was also observed when offspring were reared in the laboratory. Another genetic factor affecting body size was phylogenetic difference. In general, adults of south-clade populations were smaller in body size, developed smaller numbers of ovarioles, produced slender egg pods, and had fewer eggs per pod than those of north-clade populations.

Compared to solitary G0 adults, group-reared G1 adults under a short-day photoperiod exhibited a decrease in mean body size in females and an increase in males. These changes are associated with phase polyphenism and the typical responses of this locust to crowding, as previously documented by Uvarov (1966) and Farrow and Colless (1980). Solitary (isolation-reared) nymphs of this locust undergo 5 or 6 molts, while gregarious (group-reared) nymphs undergo 5 molts (Uvarov 1966, H. Tanaka 1982, Shimizu et al. 2012). Therefore, the reduction in body size in females may be partly explained by the reduced frequency of individuals undergoing 6 molts, but this trend is not observed in males, as they typically undergo 5 molts even in the solitary phase. By contrast, under a long-day photoperiod, a significant change in body size was observed in males but not in females in G1. As indicated in Table 3B, adult body size was larger under a long-day photoperiod than a short-day photoperiod. Consequently, even under crowded conditions, females exposed to a long-day photoperiod remained relatively large, resulting in no significant change in body size in G1.

*Reproductive traits related to body size.*—A positive relationship between female body size and fecundity has been documented in many insects (Honěk 1993). This relationship was also observed among different populations of the migratory locust: larger female adults developed more ovarioles, larger egg pods, and more eggs per pod, although it did not influence progeny size. Locusts produce several egg pods during their lifespan (Uvarov 1966). Under semi-natural conditions, solitary female locusts produce 3–9 egg pods (Tanaka et al. 1993). However, in the present study, lifetime fecundity was not determined. In this species, and in the red locust *Nomadacris septemfasciata* (Audinet-Serville, 1883), the number of ovarioles is determined in the embryo and is influenced by parental crowding conditions (Albrecht et

**Table 3.** Summary of correlations between head widths and latitudes in *Locusta migratoria* reared at LD12:12 h and LD 16:8 h (30°C) in G1 (A) and G2 + G3 (B).

(A)										
Origins	Sex	N	LD12:12 h			Sex	N	LD16:8 h		
			r	R <sup>2</sup>	p			r	R <sup>2</sup>	p
All localities	♀	60	0.52	0.27	<0.001	♀	31	0.44	0.19	<b>0.013</b>
	♂	60	0.42	0.17	<0.001	♂	31	0.25	0.06	0.178
North clade	♀	47	0.10	0.01	0.493	♀	25	-0.11	0.01	0.604
	♂	47	-0.13	0.02	0.376	♂	25	-0.29	0.09	0.159
South clade	♀	13	-0.44	0.20	0.131	♀	13	-0.44	0.20	0.131
	♂	13	-0.64	0.41	<b>0.016</b>	♂	13	-0.64	0.41	<b>0.018</b>
Univoltine zone	♀	13	-0.73	0.53	<b>0.004</b>	♀	8	-0.85	0.72	<b>0.005</b>
	♂	13	-0.80	0.63	<0.001	♂	8	-0.91	0.82	<b>0.008</b>
Uni to bivoltine zone	♀	13	0.87	0.76	<0.001	♀	9	0.81	0.66	<b>0.006</b>
	♂	13	0.90	0.81	<0.001	♂	9	0.70	0.49	<b>0.033</b>
Bivoltine zone	♀	13	-0.85	0.73	<0.001	♀	5	-0.90	0.81	<b>0.036</b>
	♂	13	-0.94	0.89	<0.001	♂	5	-0.74	0.55	0.175
Bi to trivoltine zone	♀	17	0.60	0.36	<b>0.009</b>	♀	9	0.68	0.46	<b>0.043</b>
	♂	17	0.57	0.32	<b>0.015</b>	♂	9	0.67	0.45	<b>0.048</b>

(B)										
Origins	Sex	N	LD12:12 h			Sex	N	LD16:8 h		
			r	R <sup>2</sup>	P			r	R <sup>2</sup>	P
All localities	♀	53	0.34	0.12	<b>0.012</b>	♀	43	0.39	0.16	<b>0.008</b>
	♂	53	0.17	0.03	0.239	♂	43	0.18	0.03	0.239
North clade	♀	34	-0.23	0.05	0.187	♀	36	-0.20	0.04	0.257
	♂	34	-0.42	0.17	<b>0.013</b>	♂	36	-0.36	0.13	<b>0.029</b>
South clade	♀	19	-0.33	0.11	0.177	♀	7	-0.32	0.10	0.501
	♂	19	-0.32	0.10	0.185	♂	7	-0.43	0.19	0.351
Univoltine zone	♀	12	-0.83	0.68	<0.001	♀	10	-0.80	0.64	<b>0.004</b>
	♂	12	-0.71	0.51	<b>0.007</b>	♂	10	-0.63	0.39	0.052
Uni to bivoltine zone	♀	7	0.64	0.41	0.127	♀	7	0.64	0.41	0.127
	♂	7	0.49	0.24	0.285	♂	7	0.49	0.24	0.285
Bivoltine zone	♀	11	-0.73	0.53	<b>0.009</b>	♀	9	-0.58	0.34	0.104
	♂	11	-0.71	0.51	<b>0.011</b>	♂	9	-0.50	0.25	0.182
Bi to trivoltine zone	♀	12	0.64	0.41	<b>0.024</b>	♀	14	0.54	0.29	<b>0.047</b>
	♂	12	0.58	0.33	<b>0.049</b>	♂	14	0.55	0.30	<b>0.040</b>

Bold characters indicate  $p < 0.05$ . Data are based on Suppl. material 1: table S3.

al. 1959). This observation was supported by the present results, as both G0 and G1 females showed similar numbers of ovarioles due to their mothers experiencing solitary lives during the adult stage. In contrast, G2 adults had significantly reduced numbers of ovarioles because their mothers were kept under crowded conditions.

*Phase-related traits.*—Crowding influences various traits in the migratory locust, including adult body size. A century ago, Uvarov (1921) proposed that migratory locusts occurring at low population densities are in the solitary phase, whereas those occurring at high population densities are in the gregarious phase. Between these two extreme phases, locusts show continuous variation in various morphological traits and are in the transient phase (Uvarov 1921, 1977). Various morphological traits and ratios have been used to distinguish different phases (Uvarov 1966). One of the most frequently used ratios for various locust species, particularly in desert and migratory locusts, is the F/C ratio (Uvarov 1966, Yerushalmi et al. 2001). This ratio showed a significant correlation with latitude in all generations examined. However, this correlation was mainly caused by the fact that F/C ratio was consistently higher in the south-clade populations than in the north-clade populations, suggesting some phylogenetic factor. In contrast, E/F ratio was similar across the latitudinal range and showed no consistent latitudinal pattern.

The present study confirmed that F/C ratio changes easily in response to crowding and showed significant differences between solitary G0 and group-reared G1 insects, suggesting that it is a

reliable parameter for detecting morphological gregarization within populations of migratory locusts. As suggested by Gunn and Hunter-Jones (1952), in the laboratory, F/C ratio may not reach the values of gregarious adults observed in the field. Most of the Japanese populations used in this study had no record of gregarization in the field, except for a few populations in which gregarization lasted only for 1 or 2 years. The F/C ratio recorded in those populations ranged from 3.03 to 3.30 in females and 3.09 to 3.49 in males (Ito and Yamagishi 1976, A. Tanaka 1987, Yamagishi and Tanaka 2009). These values are larger than some of those recorded in gregarious populations (2.85 to 3.12 in females and 2.95 to 3.24 in males based on Farrow and Colless 1980). In this study, the mean values in G1 reared at LD 12:12 h were 3.33 and 3.51 in females and males, respectively (Suppl. material 1: table S2). These values suggest that the degree of gregarization was smaller in the laboratory than that recorded for gregarized populations in the field. Several factors might be responsible for this difference, including the number of locusts per cage, temperature, and phase accumulation (Gunn and Hunter-Jones 1952). The density effects on morphometric traits are known to be cumulative over 2 or 3 generations (Uvarov 1966). However, in this study, both F/C and E/F ratios remained similar across G1–3.

*Sexual size dimorphism.*—The present study confirmed that adult body size is larger in females than in males of the migratory locust (Uvarov 1966, Farrow and Colless 1980). In a previous study, I compared the adult body sizes of migratory locusts collected during

different years at a single locality and found no significant correlation between the two sexes (Tanaka 2022). The lack of correlation within a single population is likely due to phenotypic variation in body size in response to annual changes in environmental factors, as noted by Whitman (2008). In this study, I analyzed the adult body sizes of the two sexes among geographically different populations and found that SSD tended to increase in field-collected individuals as females became larger. Because migratory locusts are female-biased species, this result is opposite to Rensch's rule, which was originally applied for vertebrates: SSD should increase with increasing body size in male-biased species and decrease in female-biased species (Rensch 1960, Blankenhorn et al. 2004, 2006). Bidau et al. (2016) reported that in 45 analyzed orthopteran species, Rensch's rule was observed in 26.7%, and a converse of Rensch's rule was observed in 17.8%. In the rest (55.5%), the male and female body sizes scaled isometrically. The sex difference in body size was greatly reduced when offspring were reared in a group, but the above trend was maintained in G1–3, with males being relatively smaller than females in populations with larger body sizes.

Migratory male locusts develop slightly faster than females (Hochkirch and Gröning 2008, Whitman 2008), but the protandry often associated with short nymphal development and small body size in males may not be so important in this locust because sexual maturation requires a few weeks, mating takes place more than once, and the  $P^2$  (i.e., the proportion of offspring sired by the last male to mate) is high (approximately 76% in solitary locusts and 52% in group-reared locusts, Tanaka and Zhu 2003).

Although the migratory locust assumed a saw-toothed pattern in body size, the ratio of female to male head width (female/male ratio) was positively correlated with latitude in the migratory locusts. This pattern was maintained when the locusts were reared in a group in the laboratory. The northward increase in female/male ratio means that the rate of increase in body size is smaller in males than in females. In this locust, male-female associations, such as mounting, are primarily precopulatory and have been regarded as a way of guarding the female partner until the optimal moment for sperm transfer in terms of egg fertilization (Parker and Smith 1975). Precopulatory mounting and copulation lasts for 12–18 h in an Okinawa and Ibaraki populations (Tanaka and Zhu 2003). A female locust in copula may suffer not only from a high risk of predation because she cannot escape quickly by flight when attacked (Zhu and Tanaka 2002) but also from the heavy load of a male mounting on her. Under these circumstances, a smaller male body size might be selected for at higher latitudes.

In conclusion, this study revealed a latitudinal cline in body size and morphometric ratios in the migratory locust across the Japanese Archipelago, which is similar to Masaki's clines initially described for crickets. The observed patterns suggest a complex interplay of genetic variation, growth efficiency, and environmental factors related to the length of the growing season. Additionally, social interactions and predation pressure may play a role in shaping SSD. Further research is needed to better understand the underlying mechanisms driving these patterns in locust populations.

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### Supplementary material 1

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Data type: docx

Explanation note: **fig. S1**. The proportion of *Locusta migratoria* adults and nymphs collected on August 7 at 36.9°N (site no. 9). **fig. S2**. The F/C (hind femur length/head width) and E/F (Forewing length/hind femur length) ratios of adults reared at LD 16:8 h (G1–G3). **fig. S3**. Log-transformed mean head widths of males plotted against those of females in *Locusta migratoria* adults. **table S1**. Latitude, longitude, altitude and annual mean temperature of collection sites. **table S2**. Body size parameters and morphometric ratios of *Locusta migratoria* collected at different latitudes. **table S3**. Correlations between body size and latitude in different zones with respect to life cycles in *Locusta migratoria*. **table S4**. Mean body sizes (mm) of *Locusta migratoria* adults reared in cages for three generations (G1–3) at LD 12:12 h and LD 16:8 h. **table S5**. Mean head widths of field-collected *Locusta migratoria* female adults, egg pod widths and numbers of eggs per pod in different localities. **table S6**. Head width and the number of ovarioles of field-collected and laboratory-reared *Locusta migratoria* female adults. **table S7**. Comparison of the numbers of ovarioles of *Locusta migratoria* females reared at LD 12:12 h and LD 16:8 h in the first (G1) and second (G2) generations. **table S8**. Body weight of hatchlings produced by *Locusta migratoria* adults collected in the field (A) and those produced by G1 adults reared in the laboratory (B). **table S9**. Mean duration of nymphal development per cage in the 1<sup>st</sup> laboratory generation (G1) *Locusta migratoria* at LD 12:12 h and LD 16:8 h (A) and correlation with latitude (B). **table S10**. Mean duration of nymphal development, head width, and growth efficiency in G1 *Locusta migratoria* reared at LD 12:12 h and LD 16:8 h (30°C). **table S11**. Analyses of F/C (hind femur length/head width) and E/F (forewing length/hind femur length) ratios in relation to latitudes (A, B), phylogenetic clade (C), and sex (D). **table S12**. Correlation between ratios of female head width to male head width and latitudes in field-collected (G0) and lab-reared (G1–3) migratory locusts.

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