

Occurrence of giant migratory locust *Locusta migratoria* (Acrididae) on Tsushima Island, Japan

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Academic editor: Michel Lecoq | Received 15 September 2023 | Accepted 15 December 2023 | Published 15 April 2024

<https://zoobank.org/95F08CF5-5F6B-42D0-BD4A-EC9685071200>

Citation: Tanaka S, Tokuda M (2024) Occurrence of giant migratory locust *Locusta migratoria* (Acrididae) on Tsushima Island, Japan. Journal of Orthoptera Research 33(1): 113–126. <https://doi.org/10.3897/jor.33.112789>

Abstract

This study focused on the populations of *Locusta migratoria* (Linnaeus, 1758) on Tsushima Island, Japan, which exhibited the largest mean adult body size when compared to other populations from various climatic regions. Certain individuals, designated as “giant locusts,” displayed exceptionally large sizes, with females and males identified when with head widths surpassing 10.5 mm and 8.0 mm, respectively. The maximum weight recorded for a giant locust was 8.9 g, in contrast to other examined females with the maximum weight ranging from 3.1 to 5.5 g. Notably, giant females exhibited the ability to yield larger egg pods and progeny compared to their counterparts. A positive correlation emerged between body size of adult females and the number of ovarioles. To explore the potential heritability of body size, selection experiments were conducted across two generations. A significant impact of selection on adult body size was apparent at LD 12:12h, whereas this effect was not evident at LD 16:8h. Furthermore, crossing experiments showed that body size at hatching closely resembled that of the female parent or demonstrated dimensions intermediary between the two parents, suggesting a complex genetic basis for the observed body size variations. This study provides no evidence of genetic differentiation between the giant locusts and the other locusts on this island.

Keywords

body size, egg number, climate change, genetic differentiation, ovariole number

Introduction

The migratory locust, *Locusta migratoria* (Linnaeus, 1758), is widely distributed in the Old World (Uvarov 1966, 1977, Farrow and Colless 1980, Lecoq 2022). We previously examined the phylogenetic relationships among populations in different climatic regions using a mitochondrial DNA analysis and discovered two

major clades: the north clade consists of individuals from temperate and cold–temperate areas of Japan and the Chinese continent, and the south clade comprises those from subtropical islands of Japan, Hainan Island in China, Timor-Leste, Australia, Ethiopia, France, and some individuals from Tsushima Island, Nagasaki prefecture and Honshu of Japan (Tokuda et al. 2010). The presence of the two clades in this species was supported by Ma et al. (2012) who carried out more intensive sampling and discovered that the northern European populations of the species correspond to the north clade.

During our investigation, we encountered unusually large adults of the species *Locusta migratoria* on Tsushima Island, Nagasaki prefecture, Japan, colloquially termed giant locusts. The presence of these giant locusts on the island has been documented by Japanese entomologists (e.g., Hiura 1976), and preserved specimens can be found in various Japanese museums. Farrow and Colless (1980) compiled data on the average body sizes of adult *L. migratoria* specimens collected worldwide. According to their data, based on known sample sizes, the mean head width of solitary adults falls within the range of 6.6–8.5 mm in females and 5.0–6.4 mm in males. However, as described below, certain adults found on Tsushima Island exhibited head widths exceeding 10.5 mm in females and 8.0 mm in males. This intriguing discovery prompted us to investigate the prevalence and potential causes of the existence of these exceptionally large-sized individuals.

In the course of this study, we conducted fieldwork to collect adult *L. migratoria* specimens on Tsushima Island and subsequently measured their body sizes. The primary objective was to analyze the distribution of body sizes among the adult specimens, including those classified as giant locusts (referred to as Tsushima giants [TGs]) based on the aforementioned criteria. We then proceeded to conduct a comparative analysis of the morphological, reproductive, and developmental traits of the giant individuals and their regular-sized counterparts.

In *L. migratoria*, solitary nymphs residing in sparse environments typically undergo five to seven molts (Têtefort and Wintrebert 1963, Lecoq 2022). However, in a population from Kyoto, Japan, H. Tanaka (1982) reported the observation of only five and six nymphal molts under solitary conditions. Similarly, the senior author of this study observed five and six nymphal molts under solitary conditions in various Japanese populations originating from Okinawa Island, Ibaraki, and Hachijo Island as well as in a Chinese population from Altay Prefecture in the Xinjiang Uygur Autonomous Region, China (Tanaka S, unpublished data). Notably, special attention was paid to assessing the number of nymphal molts in the giant locusts and exploring the genetic factors influencing body size.

The results of this research shed light on the genetic and morphological aspects of giant locusts and contribute to our understanding of how and why such large individuals are maintained within the population.

Materials and methods

Insects.—*Locusta migratoria* on Tsushima Island is mainly bivoltine, and adults occur in early summer and fall (Tanaka 2024). We made two trips to Tsushima Island—October 9–11 in 2008 and October 10–12 in 2012. Dr. Hironori Sakamoto collected nine specimens in 2018 and three in 2022. Locusts were caught with an insect net or by hand at nine locations on Tsushima Island (Table 1). Most individuals caught were adults, with 98.7% (N = 231) in 2008 and 88.6% (N = 263) in 2012.

Table 1. Collection sites on Tsushima Island.

Localities	Latitude (N), Longitude (E)
Tsutsu	34.11, 129.17
Uchiyama	34.16, 129.25
Kuta	34.17, 129.18
Koutsuki 1	34.18, 129.18
Koutsuki 2	34.19, 129.18
Kutamichi	34.19, 129.29
Shimobaru	34.23, 129.21
Kitasato	34.24, 129.29
Neo	34.25, 129.32

Morphometric measurements.—The captured locusts were brought to the Tsukuba laboratory where head width (C), hind femur length (F), and forewing length (E) of the adults were measured with a digital caliper (Digipa pro; Mitsutoyo Co., Kanagawa, Japan) to the nearest 0.1 mm according to the method of Dirsh (1951, 1953). The total body length (TBL) from the head to the tip of forewing of intact individuals was also measured.

Rearing and egg collection.—Some field-collected females were reared individually on leaves of *Bromus catharticus* Vahl in small nylon-screen cages (28 × 12 × 28 cm). They laid egg pods in moist sand (about 15% moisture content) held in plastic containers (340 ml in volume) following the methods outlined by Nishide and Tanaka (2019). The body weight of females was measured every day to the nearest 1 mg using an electric balance (PC440, Mettler Toledo, Tokyo, Japan) to determine the maximum body weight. Because eggs laid in the fall in this region undergo diapause, the eggs were incubated at 20°C for 30 days and then stored at 5°C for more than 3 months to break diapause (Tanaka 1992, 1994).

Comparison of head widths of *L. migratoria* between Tsushima and other regions.—The mean head widths of adult females and males in the solitary phase were calculated for those collected in 2008 and 2012. Data for other regions were sourced from Farrow and Colless (1980) considering only samples with known sizes.

Measurements of various traits.—The maximum width of egg pods was measured two days after deposition using a digital caliper. Hatchling body weight was measured by weighing 5–20 hatchlings held in a plastic tube (volume = 1.5 ml) 6–12 h after hatching to the nearest 0.1 mg using an electric balance (AT201, Mettler Toledo, Tokyo, Japan). The number of eggs was recorded based on the number of hatched nymphs and dead eggs left in each pod. The number of ovarioles per female adult was determined by doubling the number of ovarioles in the right ovary. No significant difference was observed in the number of ovarioles in the right and left ovaries of females (Tanaka 2023). Hatchling body weight was determined by weighing approximately 10 hatchlings held in a plastic tube.

The head widths of all dry specimens (12 females, 4 males) collected on Tsushima Island in late July and late September 1930 and 1933 and preserved at Kyushu University Museum were measured. Given their status as dry specimens, they were analyzed separately from the live samples. Hiura (1976) documented the total body lengths of specimens from 1967 to 1975, and their head widths were estimated using a second-order equation based on fresh specimens from this study (Suppl. material 2).

Rearing of progeny in the laboratory.—Hatchlings obtained from egg pods laid by a field-collected TG female with a head width of 11.3 mm were individually raised in small cages at LD 12:12h or LD 16:8h maintained at a temperature of 30°C. These photoperiods roughly correspond to the fall and summer daylengths, respectively, in central Japan. The date of ecdysis was recorded for each individual. All hatchlings underwent individual weighing using the previously outlined method. Upon reaching adulthood, each individual was weighed to the nearest 1 mg, and subsequently, their head width was measured three to five days after adult emergence. Hatchlings originating from field-collected females (designated as generation 0 [G0]) were reared separately in groups of 100 to 200 individuals within a larger cage (42 × 22 × 42 cm). These hatchlings, referred to as generation 1 (G1), were exposed to the same photoperiodic conditions (LD 12:12h or LD 16:8h) and temperature (30°C) as described earlier. The head widths of the emerged adult insects were recorded. Eggs obtained from each family lineage reared at LD 12:12h were subjected to a range of temperatures, as previously described, to terminate diapause. Upon hatching, these eggs were reared under the same conditions as mentioned above (30°C) to evaluate the head width of the resulting second-generation adults. Notably, the collection of eggs at LD 16:8h was omitted due to the known tendency for suppressed reproductive activity under long photoperiods in Japanese strains of *L. migratoria*, a phenomenon documented by Tanaka et al. (1993), H. Tanaka (1994), and Hasegawa and Tanaka (1996). In certain cages, newly emerged adult insects were weighed subsequent to a 24-hour period of being housed without access to food.

Selection experiments.—Approximately 100 hatchlings derived from a field-collected TG female with a head width of 11.3 mm were reared in a group, and the 5 largest and 5 smallest female and male adults were kept in the same cage to obtain egg pods. Egg pods obtained were handled to terminate diapause as described

above, and approximately 100 nymphs in the following generation (G1) were reared in a large cage at LD 12:12h. No attempt was made to obtain eggs at LD 16:8h because reproduction is often suppressed under crowded conditions during a long photoperiod in Japanese strains of *L. migratoria* (H. Tanaka 1994). The above procedure was repeated, and nymphs in the second generation (G2) were reared either at LD 12:12h or LD 16:8h. Upon adult emergence, head widths were measured and compared.

Crossing experiments.—Using the first laboratory generation reared in a group at LD 12:12h, four reciprocal crosses were made between a giant family (TG) and other families, including two families from Koutsuki (KO1) and two families from Neo (NE). In each cross, 10 females and 10 males were kept in a cage (42 × 22 × 42 cm) to obtain eggs. Eggs obtained from these crossings were handled as described above to terminate diapause. Hatchlings were weighed as described above.

Statistical analyses.—Head width, egg pod width, egg number, ovariole number, and hatchling body weight were analyzed using *t*-test, Tukey's multiple comparison test, and Mann-Whitney's *U*-test. Normal distribution of head widths was determined using D'Agostino and Pearson tests. Pearson's correlation coefficients were calculated for the linear relationships between various traits. 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), StatView (SAS Institute Inc., NC, USA) or Prism (GraphPad, California, USA).

Results

Body size of Tsushima populations compared with other populations of *L. migratoria*.—The head widths of solitary populations, both female and male, exhibited a strong positive correlation across a wide range of climatic regions (Fig. 1, $r = 0.87$, $N = 26$, $p < 0.001$). The linear regression analysis encompassing all data yielded the equation y (male head width, mm) = $0.84x$ (female head width, mm) - 0.71, with an R^2 value of 0.76. Among the examined populations, the combined data from Tsushima Island recorded the largest measurement, highlighted by the red data point in Fig. 1.

Variation in body size in Tsushima populations.—A summary of the measurements of body dimensions of all fresh specimens collected during this study is given in Suppl. material 1: table S1. The head width of fresh specimens combined was significantly larger in females (mean = 8.7 mm, $N = 175$) than in males (mean = 6.6 mm, $N = 275$, Mann-Whitney's *U*-test, $p < 0.001$, Fig. 2A, B). Head widths and total body lengths showed a high correlation ($r = 0.98$, $N = 446$, $p < 0.001$), with the linear regression line being highly significant (y TBL, mm = $0.621x$ Head width, mm + 10.824) (Fig. 2C). In contrast, the D'Agostino and Pearson tests did not support the presence of normal distribution in either sex ($p = 1.43$ and 0.15 in females and males, respectively). The several largest values of head width (> 10.5 mm, Fig. 2D) were apparently deviated from the majority in females, whereas only two points deviated in males (> 8.0 mm, Fig. 2E) according to the Tukey's method. In the following account, we call adults larger than these values giant locusts. The dry specimens collected in 1930 and 1933 (black bars in Fig. 2A, B) were significantly larger in both females (mean = 10.8 mm, $N = 13$) and males (mean = 7.5 mm, $N = 3$) than the fresh specimens (Mann-Whitney's *U*-test, $p < 0.05$ in each sex). The largest female and male dry specimens had head widths of 11.9 mm

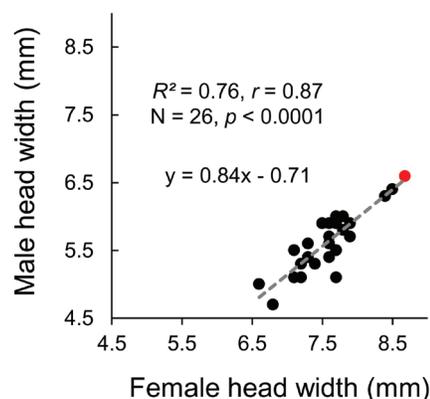


Fig. 1. Mean head widths of male and female solitary adults of *Locusta migratoria* across diverse climatic regions. Data for Tsushima populations were derived from this study (red circle) and Farrow and Colless (1980).

and 9.0 mm, respectively. The head widths estimated from TBLs reported by Hiura (1976) also showed a large mean value in both females (11.7 mm, $N = 10$) and males (8.4 mm, $N = 12$), and the largest female and male had head widths of 11.9 mm and 9.9 mm, respectively. Fig. 3 shows a comparison between a giant female (A, TBL = 80.0 mm, head width = 11.7 mm) and an average-sized female (B, TBL = 65.0 mm, head width = 8.8 mm) of the Tsushima Island populations. Giant adults were collected at various locations including Kitasato, Neo, Koutsuki 2, Kutamichi and Tsutsu in 2008 and 2012 (Suppl. material 1: table S1).

Characteristics of giant locusts.—Field-collected female adults deposited egg pods at intervals of 4–7 days (mean = 4.2 days, $SD = 0.6$ days, $N = 34$) at 30 °C, and the maximum body weight observed a day or two before oviposition was a function of head width (Fig. 3C). The maximum body weight for a giant individual with a head width of 11.3 mm was 8.91 g, while it was 4.47 g (range 3.09–5.49 g, $N = 33$) for other individuals.

Larger females tended to deposit larger egg pods ($r = 0.54$, $N = 105$, $p < 0.05$, Fig. 4A), and this tendency was also observed after the data for the giant locust were excluded ($r = 0.25$, $N = 102$, $p < 0.01$). Larger females also produced more eggs per egg pod ($r = 0.42$, $N = 79$, $p < 0.001$, Fig. 4B). The mean number of eggs per pod (\pm SD) was 113.4 ± 11.5 ($N = 9$) for giant locusts and 87.6 ± 11.6 ($N = 70$) for the other locusts, and the difference was statistically significant ($t = -6.32$, $DF = 10$, $p < 0.0001$). In this case, however, the correlation between the two variables became insignificant after the data for giant locusts were excluded ($r = 0.02$, $N = 70$, $p = 0.30$). Neither female head widths nor numbers of eggs per pod significantly affected egg mortality ($p > 0.05$ each, Suppl. material 3). Mean egg mortality (\pm SD) was $6.2\% \pm 4.1\%$ ($N = 5$) for giant locusts and $5.5\% \pm 7.9\%$ ($N = 34$) for the other locusts, and the difference was insignificant (Mann-Whitney's *U*-test, $p > 0.05$).

The number of ovarioles in female adults collected at seven distinct sites ranged from 100 to 160, with a mean of 124.2 ($SD = 12.9$, $N = 49$, Fig. 4C). The mean head width of these females was 9.1 mm ($SD = 0.8$ mm, with a range of 7.6–11.3 mm, $N = 49$). Notably, a significant correlation was observed between these two variables; larger females tended to possess a greater number of ovarioles. Among them, the two giant females had 134 and 160 ovarioles.

In G1 females, originating from a giant female with a head width of 11.3 mm, a positive relationship between their head

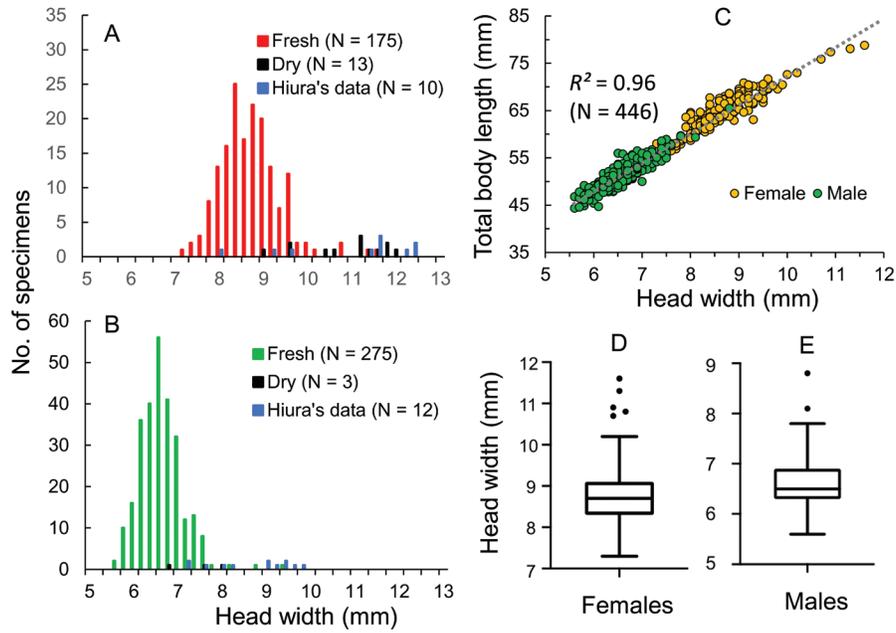


Fig. 2. Head width analysis of adult *Locusta migratoria* from Tsushima Island. Frequency distribution of head widths among female (A) and male (B) individuals. Relationship between head widths and total body length in fresh specimens (C). Box plot illustrating head width distribution by fresh female individuals (D) and male individuals (E). The figure presents data obtained from both recently collected fresh specimens and dry specimens gathered in 1930 and 1933 that were preserved at Kyushu University’s museum. Additionally, reference data from Hiura’s study (1976) are included.

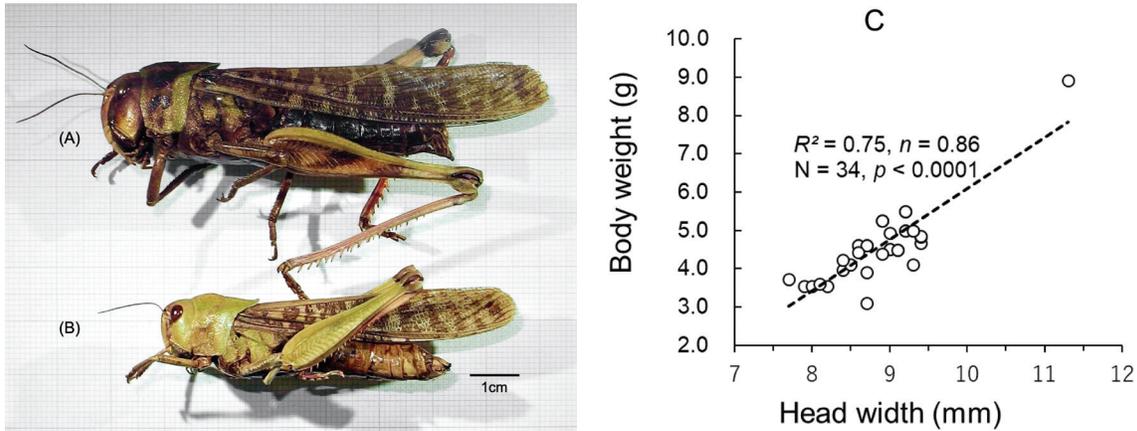


Fig. 3. A photograph showing differences between a giant female (A, TBL = 84.0 mm, head width = 11.7 mm) and an average-sized female (B, TBL = 65.0 mm, head width = 8.8 mm) of Tsushima Island. Relationship between maximum body weight and head width of *Locusta migratoria* female adults collected on Tsushima Island in 2008 and reared individually at 30°C and LD 12:12h (C). The maximum body weight for a giant individual with the head width of 11.3 mm was 8.91 g, whereas it was 4.47 g (range, 3.09–5.49 g, N = 33) for the other individuals.

widths and the number of ovarioles was evident under isolated conditions (Fig. 4D). In comparison to G0, these G1 females maintained a larger head width (mean ± SD = 10.3 ± 0.6 mm, N = 15; $t = -5.66$, DF = 62, $p < 0.0001$). However, there was a significant decrease in the number of ovarioles (mean ± SD = 114.5 ± 0.6 mm, N = 15; $t = 2.77$, DF = 62, $p < 0.01$).

Furthermore, egg pods generated by field-collected female adults from four distinct populations were found to produce hatchlings that exhibited a significant positive correlation with the head width of the females. This observation suggests that, on average, larger females had a propensity to yield larger offspring ($r = 0.73$, N = 33, $p < 0.0001$, Fig. 4E).

Nymphal growth and body size under isolation-reared conditions.—Nymphs that emerged from egg pods laid by a field-collected giant female exhibited five or six stadia in both sexes at LD 12:12h (Table 2A). The occurrence of six stadia was significantly more common in females (54.5%, N = 44) than in males (12.0%, N = 25, $\chi^2 = 12.1$, DF = 1, $p < 0.05$). The growth patterns of nymphs from both molting groups were similar during the initial three stadia, after which differences in duration emerged from the fourth stadium onwards. However, there was no significant disparity between the two molting groups during the penultimate or final nymphal instar (Table 2B). The overall nymphal development period was notably longer in females with six stadia compared to those with

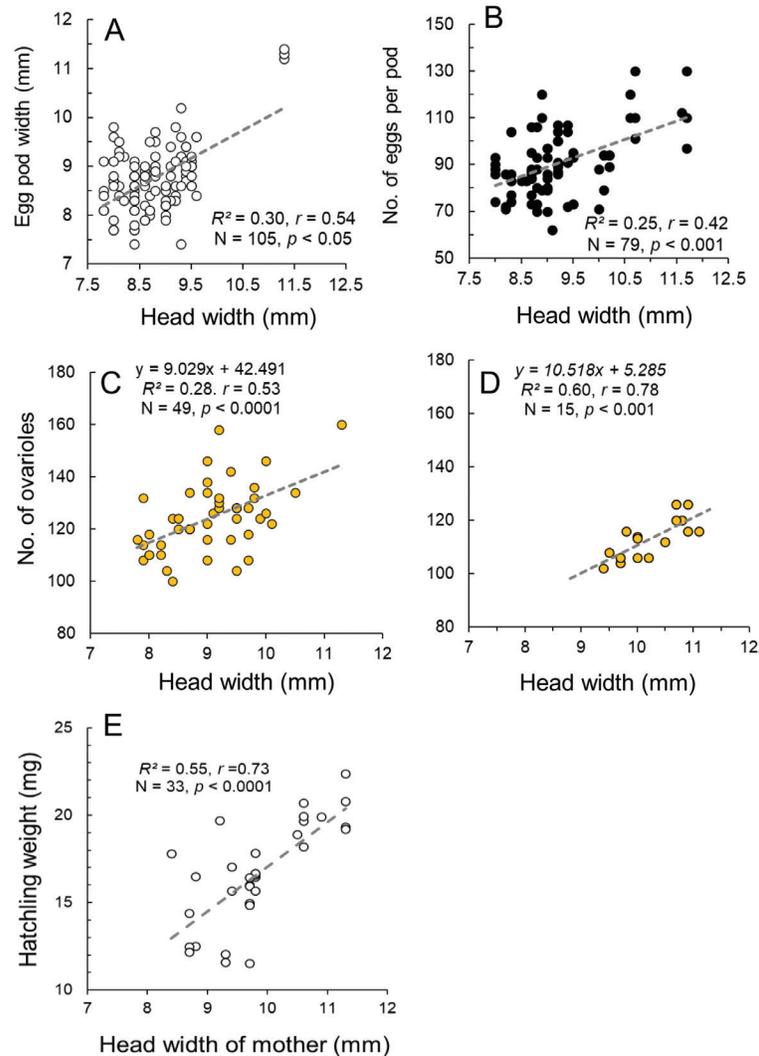


Fig. 4. The effects of female body size on egg pod width (A) and numbers of eggs per pod (B) in field-collected *Locusta migratoria*. Female adults used in (A) and (B) were collected in 2008 and 2012, respectively. Relationship between the number of ovarioles and head width in *Locusta migratoria* females collected in 2008 (C) and between the number of ovarioles and head width in G1 females of a giant family reared under isolated conditions (D). Relationship between hatchling body weight and head width of 12 *Locusta migratoria* maternal specimens collected on Tsushima Island in 2008 (E). In (E) each circle is based on 12.7 hatchlings on average.

five ($p < 0.05$, Table 2A). Similar results were observed at LD 16:8h (Table 2C, D). More females exhibited six stadia (59.6%, $N = 47$) compared to males (3.9%, $N = 51$, $\chi^2 = 35.7$, $DF = 1$, $p < 0.05$). No significant differences between the two molting groups were noted across photoperiods for either females ($\chi^2 = 0.2$, $p > 0.05$) or males ($\chi^2 = 1.0$, $p > 0.05$).

Combining the two molting groups, females exhibited shorter development times at LD 12:12h (mean \pm SD = 32.3 ± 3.0 days, $N = 44$) compared to LD 16:8h (34.3 ± 2.9 days, $N = 47$; $t = -3.27$, $DF = 88$, $p < 0.01$), while no significant difference was observed in males (30.1 ± 2.3 days, $N = 32$ at LD 12:12 h; 31.0 ± 2.7 days, $N = 51$ at LD 16:8h, $p > 0.05$).

Notably, body weight at adult emergence displayed no significant correlation with the time of adult emergence, regardless of molting groups or sex at LD 12:12 h (Fig. 5A, $p > 0.05$). Conversely, the two variables exhibited a significant negative correlation at LD 16:8 h in both sexes with five stadia, and in females with six stadia (Fig. 5B, $p < 0.05$), suggesting that longer nymphal development led to smaller adult body sizes within the same molting group.

In the aforementioned experiment, initial body weight or hatchling body weight showed similarities between females and males at either photoperiod (Table 3). At LD 16:8 h, females with five stadia (mean = 21.8 mg) exhibited significantly greater weight at hatching than those with six stadia (mean = 19.9 mg; Mann Whitney U -test, $z = -3.22$, $p < 0.05$) and males with five stadia (mean = 20.1 mg, Mann Whitney U -test, $z = -3.29$, $p < 0.01$, Table 3), indicating a tendency for smaller hatchlings in females to undergo additional molting.

Hatchling body weight did not significantly affect the duration of nymphal development in either sex at LD 12:12h (Fig. 5C) and in males at LD 16:8h (Fig. 5D). In females at LD 16:8h, however, a significant negative correlation was observed between hatchling body weight and the duration of nymphal development ($r = 0.31$, $N = 60$, $p < 0.05$, Fig. 5D), suggesting that the heavier the hatchling weight, the shorter the duration of nymphal development. However, no significant correlation was observed between the two variables when the individuals in different molting groups were separately analyzed at either photoperiod (Suppl. material 1: table S2).

Table 2. Duration of nymphal stadia (mean ± SD, days) for *Locusta migratoria* reared individually at LD 12:12h (A, B) and LD 16:8h (C, D) photoperiods at 30°C, originating from a field-collected female with a head width of 11.3 mm.

A. Comparison at each stadium					
LD 12:12h	Molt type				ANOVA
Stadium	Females		Males		
	5	6	5	6	
1	5.3 ± 0.6 (20)	5.3 ± 0.4 (24)	5.2 ± 0.4 (22)	5.0 ± 0.0 (3)	<i>p</i> = 0.37
2	4.9 ± 0.7 (20)	4.8 ± 0.8 (24)	4.9 ± 0.5 (22)	5.0 ± 0.0 (3)	<i>p</i> = 0.89
3	4.7 ± 1.3 (20)	4.1 ± 0.6 (24)	4.6 ± 0.9 (22)	3.7 ± 1.2 (3)	<i>p</i> = 0.08
4	6.4 ± 1.4 (20) a	4.7 ± 1.0 (24) b	6.7 ± 1.6 (22) a	5.0 ± 0.0 (3) ab	<i>p</i> < 0.001
5	8.9 ± 1.3 (20) a	6.2 ± 1.1 (24) b	8.5 ± 1.2 (22) a	5.3 ± 0.6 (3) b	<i>p</i> < 0.002
6		9.0 ± 1.3 (24) a		7.7 ± 0.6 (3) b	
Total duration	30.1 ± 4.3 (20) a	34.1 ± 5.7 (24) b	29.9 ± 5.4 (22) a	31.7 ± 1.3 (3) a	<i>p</i> < 0.001
B. Comparison at the penultimate and last instars					
LD 12:12h	Molt type				
	Females		Males		
	5	6	5	6	
Penultimate instar	6.4 ± 1.4 (20)	6.2 ± 1.1 (24)	6.7 ± 1.6 (22)	5.3 ± 0.6 (3)	<i>p</i> = 0.33
Last instar	8.9 ± 1.3 (20)	9.0 ± 1.3 (24)	8.5 ± 1.2 (22)	7.7 ± 0.6 (3)	<i>p</i> = 0.21
C. Comparison at each stadium					
LD 16: 8h	Molt type				ANOVA
Stadium	Females		Males		<i>p</i>
	5	6	5	6	
1	4.7 ± 0.4 (19)	4.6 ± 0.6 (28)	4.8 ± 0.5 (49)	4.7 (2)	<i>p</i> = 0.37
2	4.7 ± 0.9 (19)	4.8 ± 0.9 (28)	5.0 ± 1.3 (49)	4.5 (2)	<i>p</i> = 0.89
3	6.0 ± 1.0 (19) a	5.0 ± 0.7 (28) b	5.0 ± 0.7 (49) b	4.0 (2)	<i>p</i> < 0.01
4	6.5 ± 1.0 (19) a	5.1 ± 0.9 (28) b	6.3 ± 1.1 (49) a	5.0 (2)	<i>p</i> < 0.001
5	9.4 ± 1.4 (19) a	6.2 ± 1.2 (28) b	9.2 ± 2.2 (49) a	7.5 (2)	<i>p</i> < 0.001
6		10.5 ± 1.2 (28)		9.5 (2)	
Total duration	31.7 ± 1.9 (19) a	38.2 ± 3.4 (28) b	30.9 ± 2.7 (49) a	36 (2)	<i>p</i> < 0.001
D. Comparison at the penultimate and last instars					
LD 16: 8h	Molt type				
	Females		Males		
	5	6	5	6	
Penultimate instar	6.5 ± 1.0 (19)	6.2 ± 1.5 (28)	6.3 ± 1.1 (49)	7.5 (2)	<i>p</i> = 0.71
Last instar	9.4 ± 2.0 (19) a	10.5 ± 1.0 (28) b	9.2 ± 2.2 (49) a	9.5 (2)	<i>p</i> < 0.001

Males with 6 nymphal instars were excluded from analysis at LD 16: 8h because N = 2. Different letters indicate significant differences in mean value by the Tukey's multiple comparison test or *t*-test at the 5%. Numbers in parentheses indicate N. Bold letters indicate *p* < 0.05.

Table 3. Comparison of body weights at hatching of *Locusta migratoria* females and males undergoing 5 and 6 molts originating from a field-collected female with a head width of 11.3 mm.

	No. of molts	Hatchling wt.		
		(mg)	<i>N</i>	<i>p</i>
LD 12:12h				
Female		19.7 ± 2.8	43	<i>t</i> -test
Male		18.4 ± 2.7	25	<i>p</i> = 0.07
Females	5	20.1 ± 2.8	19	
Females	6	19.3 ± 2.6	24	ANOVA
Males	5	18.7 ± 2.7	22	<i>p</i> = 0.07
Males	6	15.9 ± 0.9	3	
LD 16: 8h				
Female		20.5 ± 2.4	60	<i>t</i> -test
Male		20.1 ± 1.7	52	<i>p</i> = 0.23
Females	5	21.8 ± 1.7 a	21	
Females	6	19.9 ± 2.4 b	39	ANOVA
Males	5	20.2 ± 1.5 b	50	<i>p</i> < 0.001
Males	6	17.8	2	

Nymphal growth and body size under group-reared conditions.—Fig. 6 illustrates variations in body weight at adult emergence plotted against the duration of nymphal development in G2 of two family lines (TG and TK) reared as a group. For males, a consistently significant negative correlation was observed between these two variables regardless of the photoperiod. For females, however, the relationship between these variables proved to be inconsistent, displaying both positive and negative correlations of varying significance. This discrepancy seems to be due to the presence of larger adults undergoing extended development. Because they were reared in a group, the number of molts was unknown. Nevertheless, the discernible pattern of changes in body size as the time of adult emergence was delayed, was especially evident within the large-sized family (Fig. 6A, B), resembling the trends seen under solitary conditions (Fig. 5B). This may imply that these individuals progressed through six nymphal stadia.

Fig. 7 illustrates the relationship between the mean duration of nymphal development and the resulting adult body weights at emergence in G2 of different family lines reared in a group at LD 12:12h (A) and LD 16:8h (B). A significant correlation was

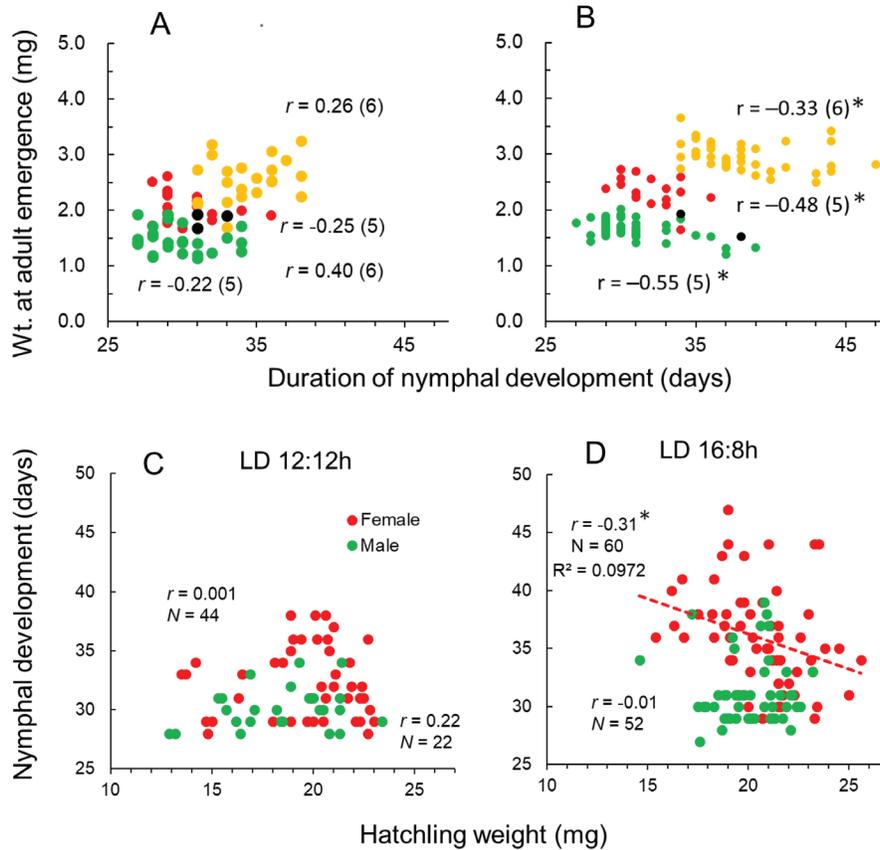


Fig. 5. Relationship between nymphal development and body weight at adult emergence in giant *Locusta migratoria* individually reared at LD 12:12h (A) and LD 16:8h (B). The numbers presented in parentheses denote the number of nymphal stadia. In (A), the sample size were $N = 20$ and 24 for females with 5 and 6 nymphal instars, respectively; and $N = 22$ and 3 for males with 5 and 6 nymphal instars, respectively. In (B), the sample sizes were $N = 19$ and 28 for females with 5 and 6 nymphal instars, and $N = 49$ and 2 for males with 5 and 6 nymphal instars. Relationship between body weight at hatching and nymphal development in giant *Locusta migratoria* individually reared at LD 12:12h (C) and LD 16:8h (D). Asterisk indicates $p < 0.05$.

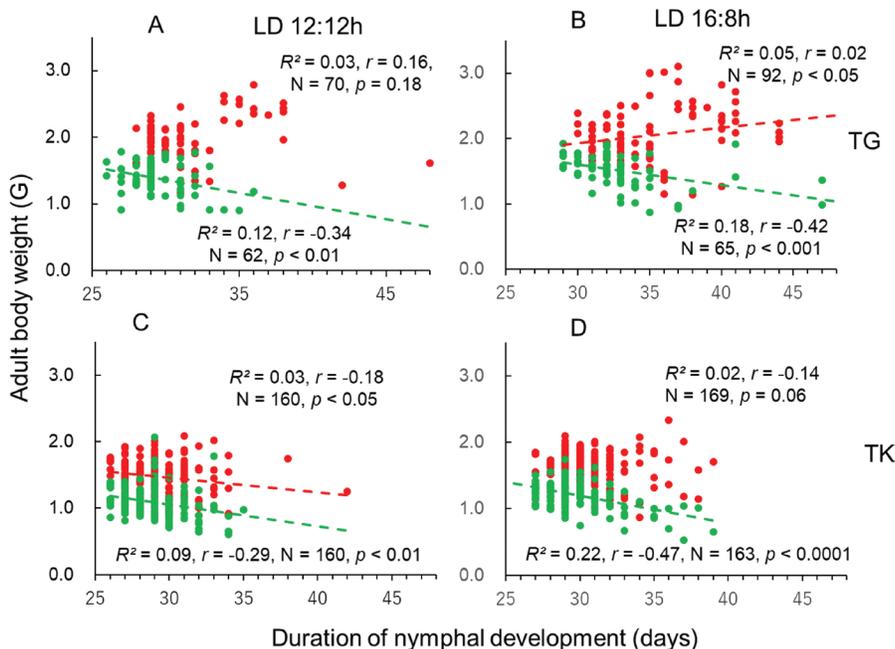


Fig. 6. Relationship between the duration of nymphal development and body weight at adult emergence in G2 of two family lines (TG and TK) reared as groups at LD 12:12h (A, C) and LD 16:8h (B, D). Each circle represents one individual, with females in red and males in green. Interrupted lines indicate statistically significant regression lines.

observed between the two variables in females, suggesting that the longer the duration of nymphal development, the larger the body weight at adult emergence. In contrast, males exhibited no significant correlation between these variables at either of the two photoperiods (Fig. 7).

When nymphs derived from different egg pods produced by field-collected females were reared separately in groups at LD 12:12h and LD 16:8h, the mean head width of the emerged adults

obtained (G1) exhibited a statistically significant positive correlation with the head width of the mother (G0) (Fig. 8A, B), suggesting that the mother's body size greatly influenced the adult body size of G1. This maternal effect persisted even in the subsequent generation (G2) derived from purebred individuals (Fig. 8C, D). Notably, in all observed instances, the field-collected giant females with a head width exceeding 10.5 mm consistently gave rise to larger offspring compared to their counterparts (Fig. 8).

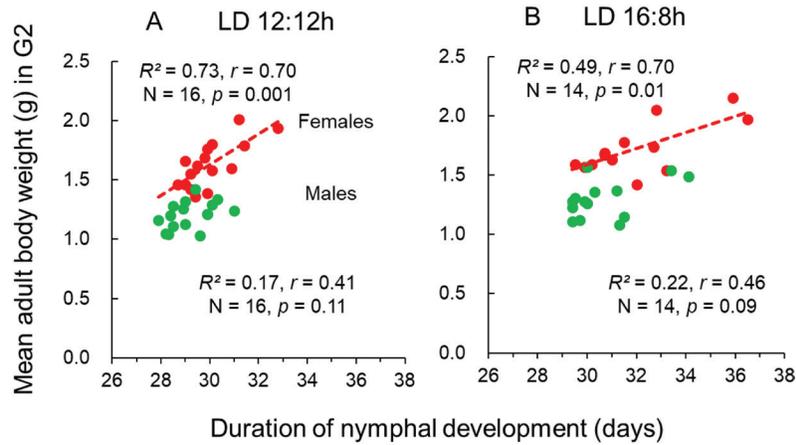


Fig. 7. Relationship between the duration of nymphal development and body weight at adult emergence in G2 of different family lines reared as groups at LD 12:12h (A) and LD 16:8h (B). Each circle represents the mean value of female (red) or male (green) individuals reared in a cage. Interrupted lines indicate statistically significant regression lines.

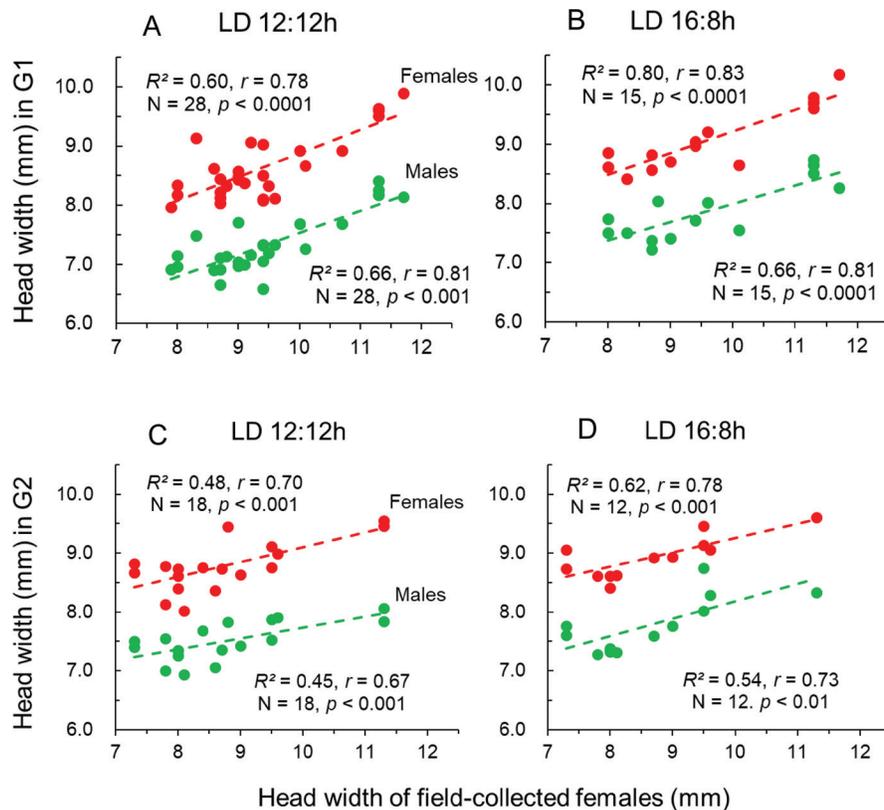


Fig. 8. Correlations of head widths between field-collected females and group-reared G1 (A, B) or G2 (C, D) adults at LD 12:12h and LD 16:8h. Each circle indicates the mean value of adults reared in a cage. In (A), mean N = 31.3 and 35.3 in females and males, respectively. In (B), N = 23.3 and 30.0 in females and males, respectively. In (C), mean N = 30.3 and 30.2 in females and males, respectively. In (D), N = 22.0 and 30.6 in females and males, respectively.

Selection for large and small adults.—After selecting for larger (L-selected) and smaller (S-selected) adults within the giant family over two generations, the mean head width in the S-selected cohort exhibited a significant reduction across both sexes (Fig. 9). This reduction was particularly pronounced when compared to the corresponding measurements taken from the L-selected group at LD 12:12h. This marked reduction in head width was not as evident when comparing the two groups at LD 16:8h conditions (Fig. 9).

Genetic control of progeny size.—In the initial lab generation, various crossings were conducted between the giant family and other family lines. Across all reciprocal crossings, the G₂ hatchling weights were either similar to the purebred lines or intermediate (Fig. 10). Notably, in two cases (Fig. 10A, C), offspring from reciprocal crossings had hatchling weights closer to the maternal mean than the paternal mean.

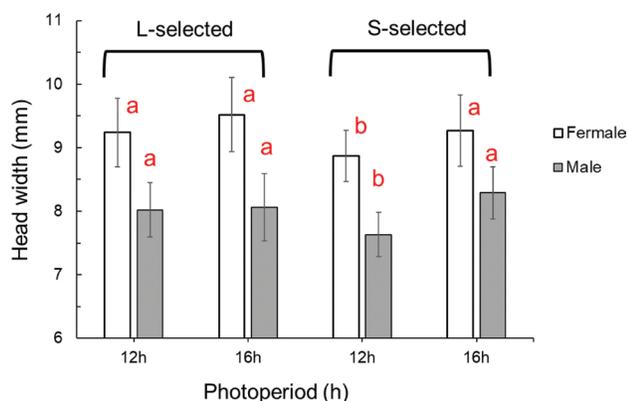


Fig. 9. Effects of selection for large (L) and small (S) adults over two generations on adult head width (mean \pm SD) in a giant migratory locust. Different letters in each sex indicate statistically significant differences at the 5% level by the Tukey's multiple comparison test.

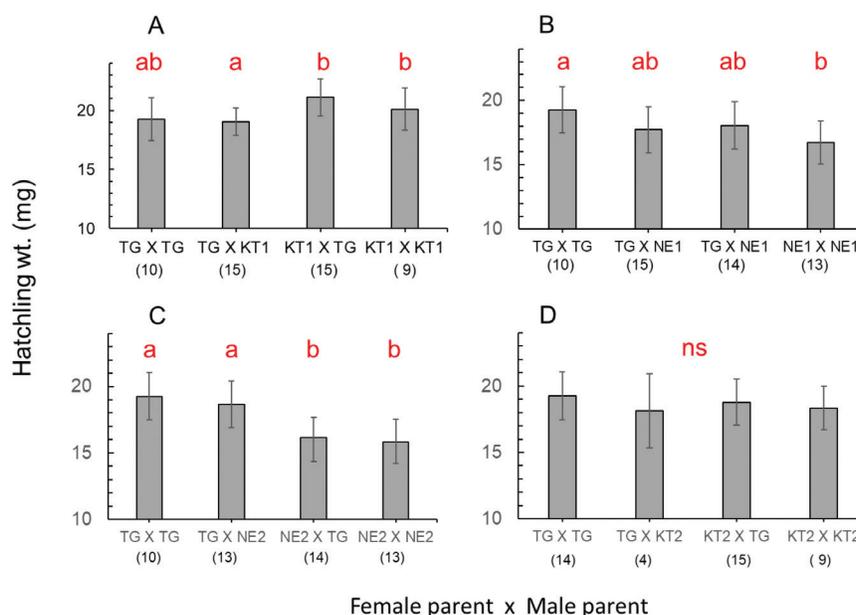


Fig. 10. Effects of reciprocal crossings between giant (TG) and other families including Koutsuki (KT1 and KT2) and Neo (NE1 and NE2) on the body weight of offspring at hatchling in F₂. Different letters in each crossing experiment indicate statistically significant differences at the 5% level using the Tukey's multiple comparison test; ns indicates no significant difference by ANOVA. Nymphs and adults of F₁ were reared as groups at LD 12:12h, and their eggs (F₂) were allowed to hatch at 30°C after diapause termination. Numbers in parentheses indicate sample sizes, with a mean of 13.8 hatchlings in each sample.

Analysis of temperature changes on Tsushima Island.—As indicated in Fig. 2, the adult body size seemed larger in specimens collected before 1976 compared to those collected after. The average air temperature on Tsushima Island increased significantly by 1.5°C, from 14.7°C in 1930 to 16.2°C in 2022. This is based on the regression line y (temperature in °C) = 0.0168x (year) - 17.8490 using data from the Japan Meteorological Agency (2022), as shown in Fig. 11A. A deeper temperature trend analysis revealed that this increase primarily occurred after 1975. This is evident when comparing 1930 to 1975 with 1976 to 2022. From 1930 to 1975, there was no significant temperature-time correlation ($r = 0.09$, $R^2 = 0.01$, $N = 46$, $p = 0.57$, Fig. 11B). However, a strong correlation emerged post-1975 ($r = 0.74$, $N = 46$, $p < 0.0001$, Fig. 11C). The temperature rise from 1976 to 2022 was 1.6°C, determined by the regression line y (temperature in °C) = 0.0346x (year) - 53.46, with an R^2 of 0.55 (Fig. 11C).

Discussion

L. migratoria from Tsushima Island showed markedly larger adult body sizes compared to other geographical populations from diverse climatic regions as documented by Farrows and Colless (1980). Among the adults collected on Tsushima Island, several displayed unusually significant size, with females weighing up to a maximum of 8.9 g. These individuals exhibited body sizes that deviated noticeably from the norm. Remarkably, these larger females (with a head width > 10.5 mm) produced notably larger egg pods and a greater number of progeny per pod compared to their smaller counterparts. In a study by Farrows (1975), the number of eggs per egg pod in solitary populations was reported to range from 66 to 116. The range observed for the giant locusts on Tsushima Island exceeded these values, ranging from 97 to 130.

In the present study, field-collected females were separated from males after collection but produced viable offspring. This suggests that they had mated at least once in the field, although we have no information about the male(s) that had mated with those females.

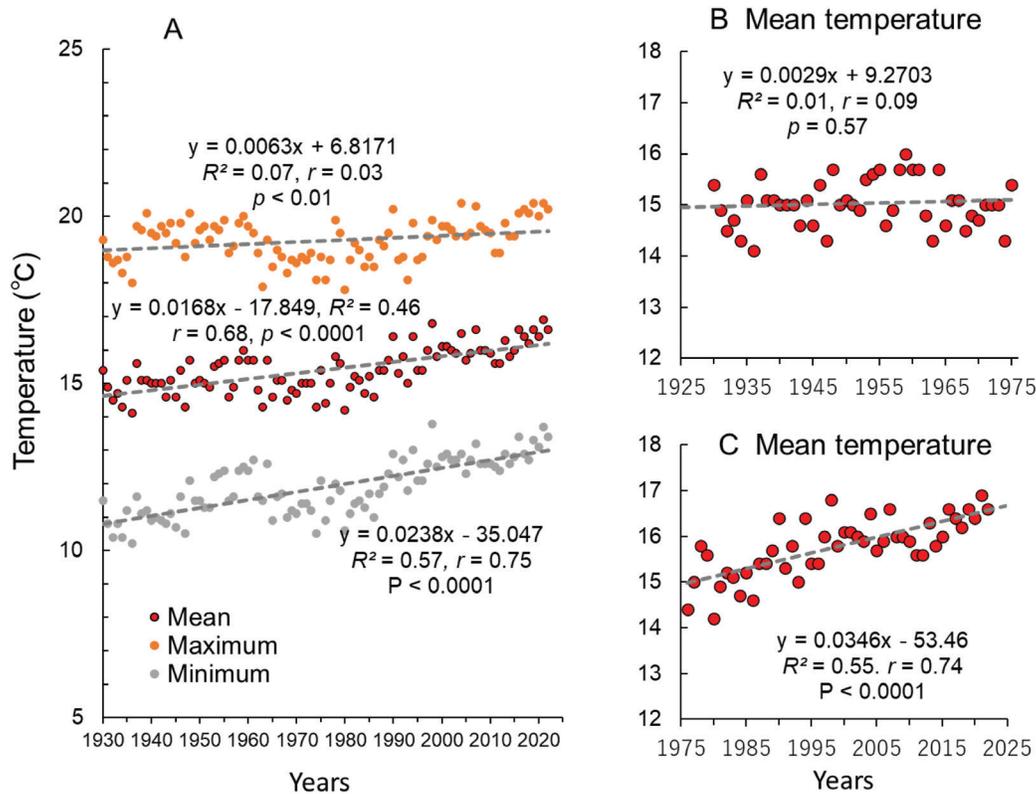


Fig. 11. Changes in annual air temperatures on Tsushima Island from 1930 to 2020 (A), from 1930 to 1975 (B), and from 1976 to 2022 (C) (Japan Meteorological Agency).

In *L. migratoria*, it has been documented that approximately 62.3% of ovarioles are utilized in egg production (N = 470, Tanaka 2024). Therefore, the presence of a positive correlation between the number of ovarioles and the size of the female body, as demonstrated in the present study, is well-founded.

Solitarious *L. migratoria* undergo five to seven nymphal stadia (Têtefort and Wintrebert 1963, Lecoq 2022). In the present study, we raised nymphs of giant locusts in isolation and observed only five and six nymphal molts. Although the giant locusts were notably larger than the other individuals on this island, none of them went through more than six nymphal stadia. Large body size was mainly observed in adults with six nymphal stadia, and such individuals were common in females but rare in males. The duration of nymphal development was longer in individuals with six molts on average than in those with five molts. However, in each molting group, body size was negatively correlated with the duration of nymphal development, suggesting that large adults tended to grow faster than small ones if the number of nymphal molts was the same.

Fig. 12 displays the relationships between hatchling body size, nymphal molt count, and adult body size in a giant family raised in isolation at LD 16:8h. Hatchlings were similar in body size between females and males. Smaller female hatchlings tended to undergo six molts, took longer to grow, and emerged as larger adults than larger hatchlings that tended to have five molts. All male hatchlings underwent five molts except for a few small hatchlings in the present study. At LD 12:12h at which nymphs grew faster and emerged as smaller adults than at LD 16:8h, no significant difference was observed in hatchling body size between the two sexes or between molting groups. These results suggest that giant locusts are likely to appear more frequently from relatively small

progeny (19.9 mg on average, Fig. 12) under long-day conditions. However, this relationship is likely to be valid only within the same family.

On the contrary, when different families were compared, a positive correlation emerged between the head width of field-collected females and the average body weight of hatchlings produced by them (Fig. 4E). This observation implies that, on average, larger females tend to give rise to offspring with greater body sizes, which exhibit a propensity to mature into larger adults (Fig. 8A, B). This maternal impact on the eventual adult body size also persisted within the purebred G2 generation. However, it is worth noting that this influence might be mitigated in natural environments due to the potential of mating with males possessing distinct genetic elements pertinent to body size. It is essential to acknowledge that the present study did not include any information regarding the potential paternal effects on this trait.

In *L. migratoria*, a positive correlation has been observed between female body size and the number of ovarioles (Tanaka 2024). This relationship was confirmed with Tsushima populations in the present study. In species such as *L. migratoria* and the red locusts *Nomadacris septemfasciata* (Audinet-Serville, 1883), the determination of ovariole numbers occurs during the embryonic stage and can be influenced by parental crowding conditions (Albrecht et al. 1959). However, within the context of this study, a noteworthy reduction in the mean number of ovarioles was observed in the G1 generation reared under solitary conditions when compared to G0 females. This contrast likely arises from the fact that the G1 generation was derived from a single family line, suggesting a potential paternal influence on this specific trait.

Four reciprocal crossings between different family lines suggested that hatchling body size was intermediate between the

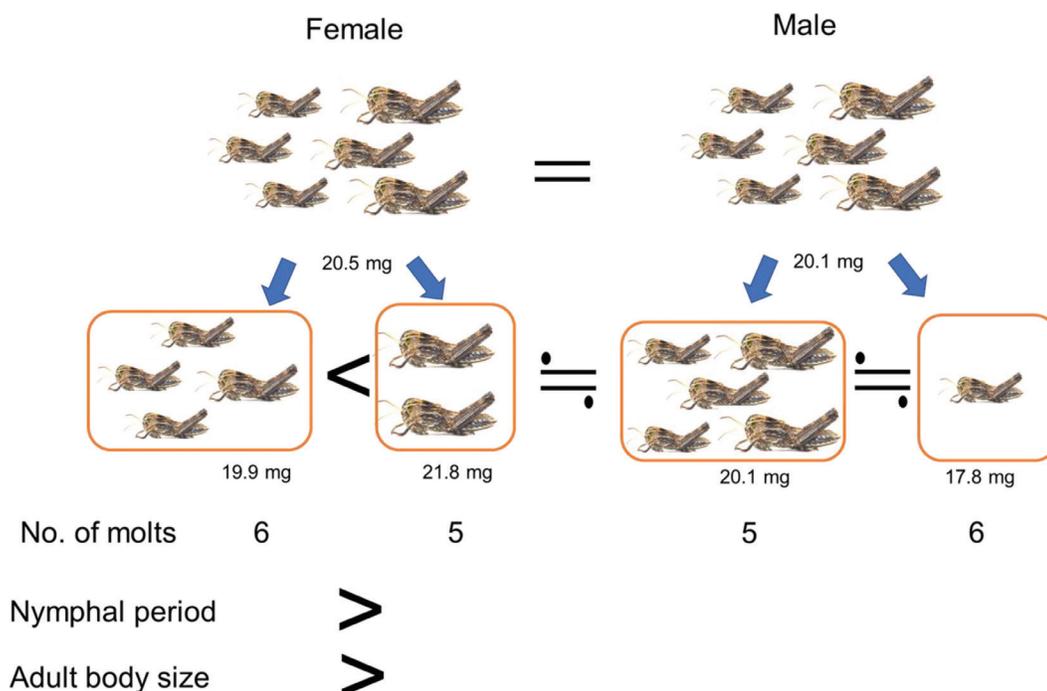


Fig. 12. Diagram illustrating how the developmental pathways of hatchlings are influenced by their initial body sizes and subsequent molt patterns, shedding light on the correlation between molting frequency, growth duration, and adult size attainment under isolated rearing conditions. On average, hatchling body size between sexes was similar. Among the female hatchlings, those with larger initial body sizes exhibited a propensity to undergo 5 molts, whereas their smaller counterparts tended to experience 6 molts during their development. Among the male hatchlings, the majority followed a pattern of 5 molts with the exception of a limited number of smaller individuals that underwent 6 molts. On average, individuals that experienced 6 molts exhibited an extended growth period but ultimately emerged as larger adults in comparison to their counterparts that underwent 5 molts. These findings are in line with the data presented in Table 1.

two parents or similar to the female rather than male parent. This phenomenon is probably related to the fact that progeny size (or hatchling body weight) and number per egg pod were positively correlated with the body size of female parents. Therefore, giant females are likely to produce large progeny and thus giant adults.

Selecting for large- and small-sized adults over two generations did not result in a further increase in body size in the former line but significantly reduced body size in both sexes in the latter line. Because the experiment was performed with a giant family line, it is possible that this line had already reached the maximum body size, and significant changes were observed only in the S-selected line. Another possibility is that the above difference was mainly caused by differences in female body size, and no significant genetic difference was involved because female body size influenced adult body size in the following generation. To determine which is the case, selection for adult body size in the two sexes should be carried out separately over extended generations.

Fig. 13 illustrates a phylogenetic relationship between TG and other individuals collected on Tsushima Island based on 2181 bp of mitochondrial sequences (originally shown in Tokuda et al. 2010). The Tsushima populations of *L. migratoria* are genetically complex, i.e., among eight individuals (TSM01-08), two (Neo, TSM01, and 06) belonged to the south clade and the other six from Neo, Kutamichi, and Unchiyama to the north clade. Of these latter six individuals, one TG individual (TSM04) was included in the analysis, and this haplotype was independently located near haplotypes obtained from Tianjin (TNJ), China (Tokuda et al. 2010). Nevertheless, at the mitochondrial DNA level, the origin of TG and its relationship with other individuals remain ambiguous. Importantly, the analysis did not provide compelling evidence for

distinguishing TG and other individuals on Tsushima Island as distinct entities. To elucidate the origin of TG, further detailed genetic analysis is needed, especially of nuclear genes between TG and other individuals.

The body sizes of *L. migratoria* collected on Tsushima Island before 1976 (Hiura 1976 and specimens deposited at Kyushu University in 1930 and 1933) were larger than those collected in the present study, as shown in Fig. 2. There are several possible reasons for this difference. One possibility is that dry specimens in the museum did not represent the body sizes at collection. Dried specimens preserved at the museum might have shrunk, but it is unlikely that they increased in size. Therefore, there is no doubt that the specimens collected in 1930 and 1933 were larger than the live specimens in this study.

A second possibility is the impact of climate change on the frequency of giant individuals. Recent warming has affected numerous organisms, including insects, in various ways (Bradshaw and Holzapfel 2001, Bale et al. 2002, Kiritani 2007, Forrest 2016, Matsuda et al. 2018). *L. migratoria* exhibits latitudinal variation in body size, known as Masaki's cline, where body size displays a saw-toothed pattern corresponding to voltinism (Tanaka 2024). The Tsushima populations are located at the southern limit of the bivoltine area and show the largest body size in this area (Tanaka 2024). To the south of this island, the body size of this locust tends to decrease southwards in the Kyushu areas where the mean air temperature and the frequency of individuals with a trivoltine life cycle increase. Therefore, recent warming might have reduced the frequency of giant locusts and produced some individuals with a trivoltine life cycle on Tsushima Island, although this has not been confirmed in the field.

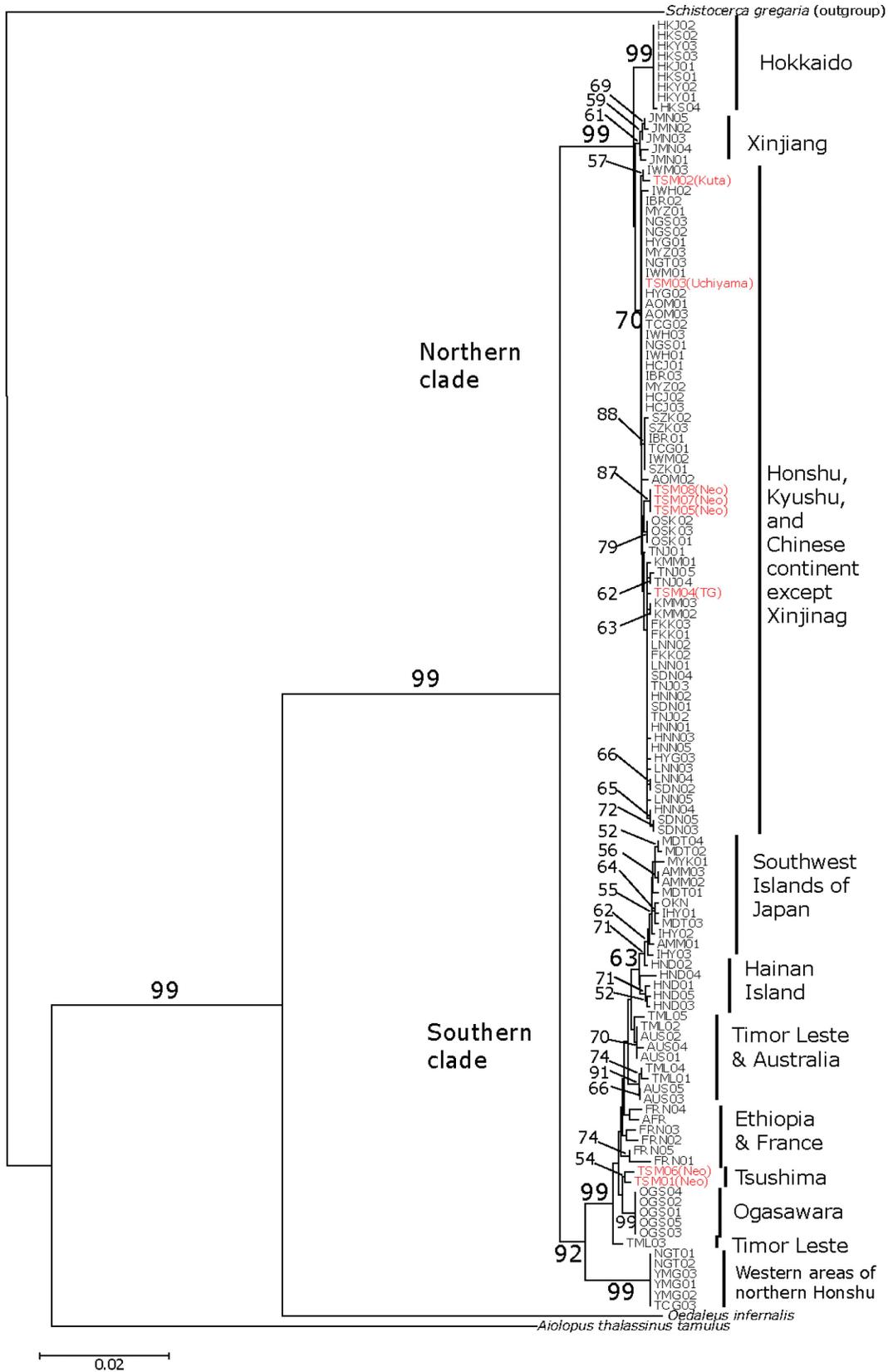


Fig. 13. Phylogenetic relationships among Tsushima Island (highlighted in red) and various other populations of *Locusta migratoria*. The original tree was constructed by Tokuda et al. (2010) using the neighbor-joining method based on a combined dataset of 2181 bp, including sequences of cytochrome b, cytochrome oxidase subunit I, NADH dehydrogenase subunit II, and 12S ribosomal RNA. Bootstrap values are provided for nodes supported by more than 50% in 1000 pseudoreplicates. This figure has been reproduced with permission and some modifications. For a detailed explanation, see Tokuda et al. (2010).

The mean air temperature on Tsushima Island has shown a notable increase of 1.5°C, rising from 14.7°C in 1930 to 16.2°C in 2022. A deeper analysis of the temperature trends revealed that this increase is primarily attributed to the rapid temperature surge observed after 1975 (Fig. 11). Consequently, there exists a plausible hypothesis that the amplified warming experienced after 1976 might have contributed to the reduction in the occurrence of giant locusts on Tsushima Island.

A third possibility may be that the mean body size of *L. migratoria* on Tsushima Island did not change significantly over the years but that the differences were mainly due to sampling errors, as the sample size was very small for both the museum specimens and the specimens reported by Hiura (1976). In a separate study, Tanaka (2022) analyzed body size changes over 16 years (2005–2020) in central Japan and found no significant variations. More comprehensive studies spanning longer periods are needed to better understand the fluctuations in body size and life cycles.

In conclusion, this study focused on the Tsushima Island populations of *L. migratoria* that contain giant individuals that are remarkably larger in terms of adult body sizes, egg size, and number when compared to geographically diverse populations. These locusts, when raised in isolation, never exceeded six nymphal stages, despite their substantial size. Particularly, larger-bodied females were more prevalent among adults with six molts, and larger adults grew faster than smaller ones within each molt category. There was a direct correlation between the head width of field-collected females and their hatchlings' mean weight, emphasizing the maternal impact on offspring traits. The results from reciprocal crossings suggest that offspring size typically resembled the female parent, indicating a likely link between giant females and the production of larger offspring and subsequent giant adults. A DNA analysis provided no evidence for the genetic differentiation between giant and other individuals that were distributed in Honshu, Kyushu, and continental China (except Xinjiang), including majority individuals on Tsushima Island. Historical data indicated that *L. migratoria* from the island before 1976 were larger than those observed in this study, possibly due to sampling errors or recent warming impacts given the significant temperature rise on Tsushima Island after 1975, which might have played a role in diminishing the prevalence of giant locusts.

Acknowledgements

We express our gratitude to Dr. Shun Kumashiro and Mr. Shun-ji Suematsu for their invaluable assistance in collecting locusts in 2013 and Dr. Hironori Sakamoto for collecting locusts in 2018 and 2020. Additionally, we extend our appreciation to Dr. Ryohei Sugahara from Hirosaki University for his valuable guidance in employing statistical methodologies. Two anonymous reviewers significantly improved the manuscript.

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Supplementary material 1

Author: Seiji Tanaka, Makoto Tokuda

Data type: pdf

Explanation note: **table S1**. Summary of measurements of *Locusta migratoria* collected on Tsushima Island on October 9–10, 2008 (A), October 11–12, 2012 (B), and September 10, 2018 (C). C, maximum head width (mm); F, hind femur length (mm); E, forewing length (mm); TBL, total body length (mm). **table S2**. The effect of initial body weight on the duration of nymphal development in the 5 and 6 molting groups in a giant *Locusta migratoria* family reared in isolation at LD 12:12h and LD 16:8h.

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Link: <https://doi.org/10.3897/jor.33.112789.suppl1>

Supplementary material 2

Author: Seiji Tanaka, Makoto Tokuda

Data type: jpg

Explanation note: **fig. S1**. Relationship between total body length and head width of fresh adult specimens of *Locusta migratoria* collected on Tsushima Island. Regression analysis indicates that the variation in head width is better explained by a second-order equation in females compared to a linear equation ($y = 0.150x - 1.036$, $R^2 = 0.85$). In males, both the second-order equation and the linear equation ($y = 0.133x - 0.273$, $R^2 = 0.78$) show similar coefficients of determination. Here, 'y' represents head width (mm) and 'x' represents total body length (mm).

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Supplementary material 3

Author: Seiji Tanaka, Makoto Tokuda

Data type: jpg

Explanation note: **fig. S2**. Relationship between egg mortality and two variables: (A) the number of eggs per pod laid by field-collected females, and (B) the head widths of these females.

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