First Record of the Occurrence and Genetics of a Short-Winged Morph in the Migratory Locust, Locusta migratoria (Orthoptera: Acrididae)

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First record of the occurrence and genetics of a short-winged morph in the migratory locust, *Locusta migratoria* (Orthoptera: Acrididae)

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Abstract

Short-winged adults appeared in the 2nd generation of inbred colonies of migratory locusts, *Locusta migratoria,* originating from Tsushima Island, Japan. Of 14 family lines, two produced several short-winged adults in the 2nd generation. These short-winged adults also had shorter hind femora than long-winged adults, indicating they may represent 'the short-winged morph' rather than monsters with abnormally short wings. The two wing morphs could be separated by the ratio of forewing length to head width. Crosses between the two wing morphs revealed that the short-winged morph was controlled by a simple recessive Mendelian unit. It is unknown whether the short-winged morph occurs in the field.

Key words

wing dimorphism, *Locusta migratoria*, recessive inheritance, migration

Introduction

Wing polymorphism is widespread among insect orders (Dingle 1996). It is usually associated with flight dispersal dimorphism. Long-winged morphs are flight-capable, whereas short-winged morphs fly little or cannot fly, although intermediate morphs may also occur in certain species (Tanaka *et al.* 2001). Many studies analyzing the evolutionary significance of wing polymorphism and polyphenism suggest the presence of trade-offs between flight capability and other developmental and reproductive traits. Long-winged morphs, which develop a flight apparatus, including long wings and flight muscles, and require the fuel and time for migratory flight, tend to delay the time to attain sexual maturity, but may enjoy the benefit of being able to reproduce in a new suitable habitat (Dingle 1985, 1996; Roff 1986; Zera & Denno 1996). In contrast short-winged morphs, which do not perform migration, may grow and reproduce more rapidly than long-winged morphs. Furthermore, short-winged females of certain species are more fecund than are their long-winged counterparts (Dingle 1985).

The migratory locust, *Locusta migratoria*, is known as a long-distance migratory insect and exhibits a phase polyphenism in which behavioral, morphological, physiological and biochemical traits vary depending on the population density (Uvarov 1966, 1977; Pener 1991; Pener & Yerushalmi 1998; Pener & Simpson 2009). Although measurable variation in various body dimensions, including wing length, is observed among different phases, all adults of this species develop long wings, and they remain strong fliers even in their solitarious forms (Uvarov 1966).

During a study on geographic variation in *L. migratoria*, adults with unusually short wings appeared in the laboratory. It was first thought that they were monsters produced in the laboratory due to endocrine disturbance, but it was also considered possible that they represent a short-winged morph.

This study was designed to characterize the morphological characteristics of this putative short-winged morph and to investigate the mechanism controlling wing-length dimorphism. It is the first report of the occurrence of a short-winged morph in the migratory locust.

Materials and methods

Insects.—Adults with markedly short wings appeared in the 2nd generation of a laboratory strain originally established from adult females collected on Tsushima Island, Nagasaki, Japan. In another study, for a specific purpose 14 family lines were established from 3-5 egg pods laid by each of 14 adult females collected on the island on October 17-18, 2008. Approximately 150 hatchlings of each family line were reared in wood-framed cages (42 × 24 × 42 cm) at 30±1°C and with a photoperiod of LD 12:12 h or LD 16:8 h, according to the method of Tanaka and Zhu (2008). Both nymphs and adults were fed with leaves of *Bromus* and bran *ad libitum*. Eggs produced by the first laboratory generation were incubated at 20±1°C for 1 month and then chilled at 10±1°C for 5 months to terminate embryonic diapause (Tanaka 1992). These eggs hatched simultaneously after incubation at 30±1°C and hatchlings were reared as described above. Adults with short wings appeared in two of the family lines. Five females and 5 males with short wings were removed from one of the family lines and kept in another cage where their eggs were collected to establish a short-winged line (SW-selected line). Eggs were also collected from another cage of the same family line from which no short-winged adults were removed (unselected line). An Okinawa albino strain that was used to cross with adults of the Tsushima strain has been described previously (Tanaka 1993).

Crossing experiments.—Tsushima short-winged male adults were crossed with Okinawa long-winged (normal) female adults to determine the genetic basis for the reduced wing length. As observed in other strains of this locust (Verdier 1969, Poras *et al.* 1983, Baehr *et al.* 1986, Hakomori & Tanaka 1992, Tanaka *et al.* 1993, Hasegawa & Tanaka 1996, H. Tanaka 1994, Okuda & Tanaka 1996), the Tsushima strain laid few eggs if kept at a long photoperiod under crowded conditions. At a short photoperiod, eggs were obtained, but they entered embryonic diapause and required a prolonged chilling before the embryos became ready to hatch. Therefore, an Okinawa albino strain, which shows no diapause at 30 °C (Hakomori & Tanaka 1992, H. Tanaka 1994), was used in this study. The albinism is controlled by a single recessive Mendelian unit (Hasegawa & Tanaka 1994). Eggs obtained from 10 Okinawa females kept together with 5 Tsushima short-winged males in a group, hatched without entering diapause at 30°C. Hatchlings obtained from 5-7

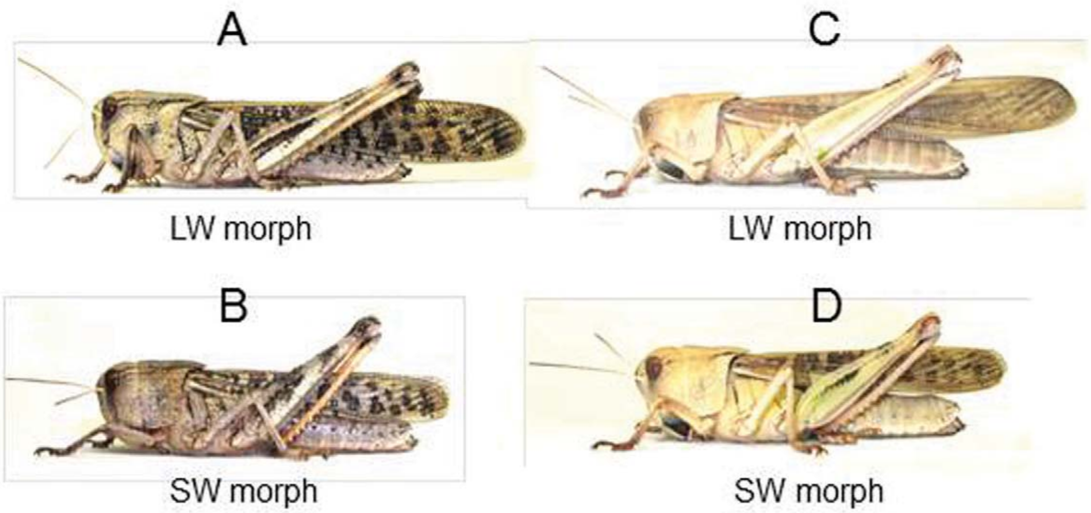

Fig. 1. Photographs showing long-winged (LW) and short-winged (SW) morphs in normal (A and B) and albino strains (C and D) of *L. migratoria*. For color version, see Plate II.

egg pods were reared in a cage, and their 2nd generations were also reared in a similar way.

Measurements of body dimensions.—The classical morphometric ratios often used to separate locusts in different phases (Stower *et al.* 1961, Uvarov 1966) were compared between long-winged and short-winged adults by measuring maximum head widths (C), hind femur lengths (F) and forewing lengths (E) with a digital caliper. In addition, a ratio of forewing length to maximum head width (E/C ratio) was determined.

Statistical analysis.—Proportions of long- and short-winged locusts were compared by a χ^2 test. Maximum head widths, hind femur lengths and forewing lengths were compared between long-winged and short-winged locusts using either a *t*-test or a covariance analysis and with Statview software (SAS Institute Inc., USA). Morphometric ratios were analyzed by a Mann-Whitney *U*-test.

Results

The incidence and characteristics of short-winged adults.—A 2nd laboratory generation of a Tsushima strain produced a mixture of adults with long (normal) and short wings (Fig. 1A, B). Their incidence under a short photoperiod was 17.7% and 9.0% in females ($n = 29$) and in males ($n = 67$), respectively, whereas it was 12.5% and 10.9% in females ($n = 64$) and in males ($n = 64$) under a long photoperiod.

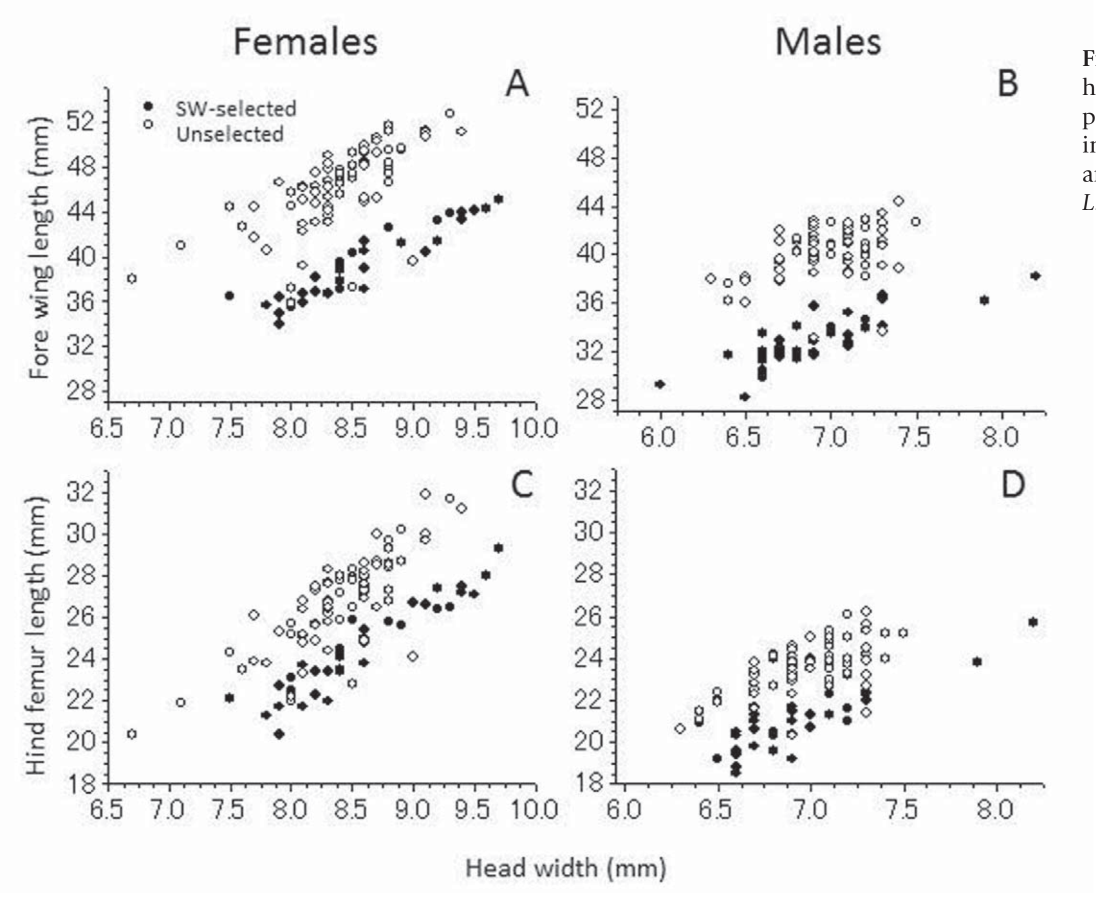

Fig. 2. Forewing (A and B) and hind femur (C and D) lengths plotted against head widths in short-wing (SW) selected and in an unselected line of a *L. migratoria* Tsushima strain.

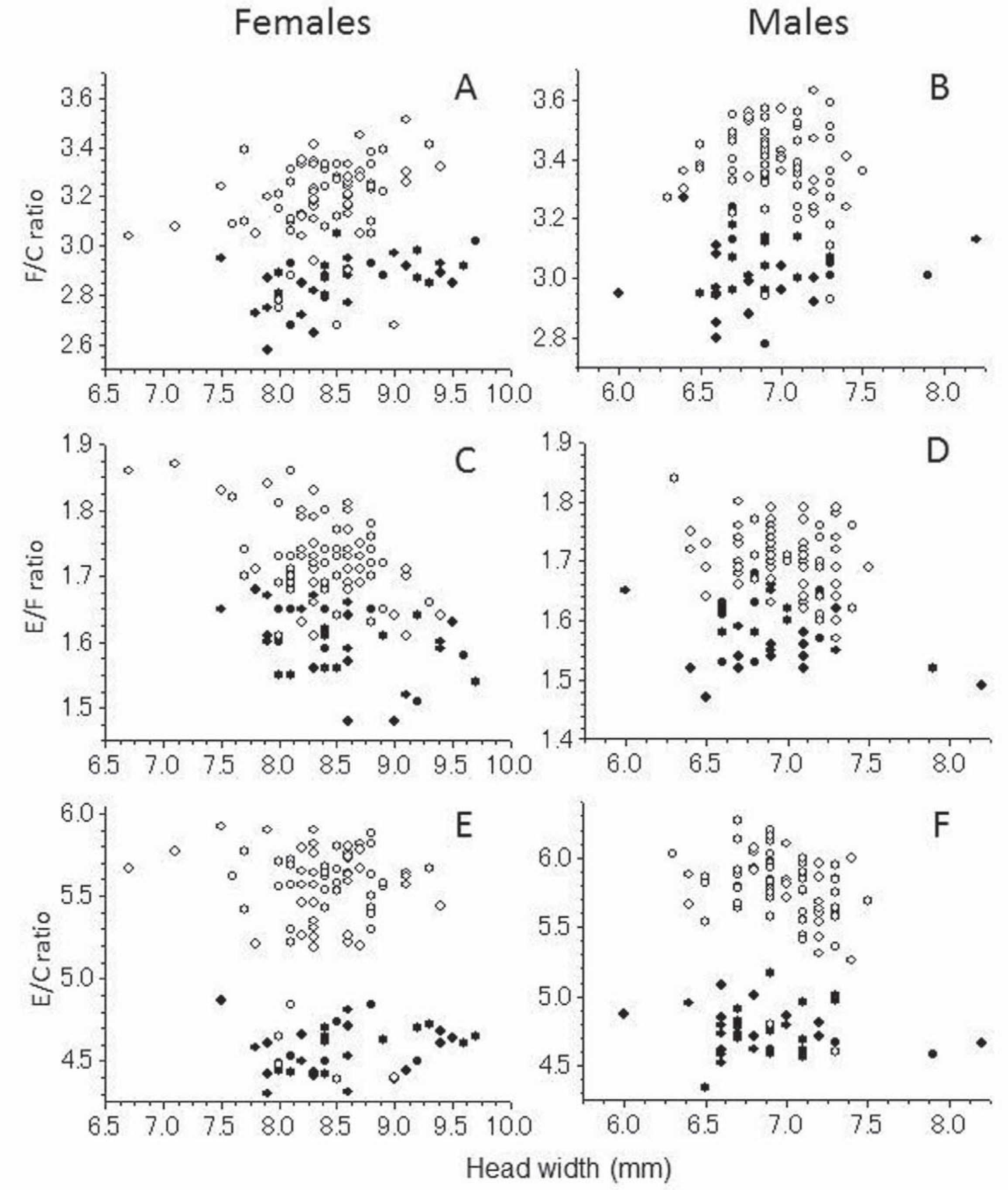

Fig. 3. F/C (hind femur length / head width), E/F (forewing length / hind femur length) and E/C (forewing length / head width) ratios plotted against head widths in a short-wing (SW) selected (●) and unselected (○) line of a *L. migratoria* Tsushima strain.

No significant difference was detected in proportions between the two sexes or between the photoperiods ($P > 0.05$, χ^2 test).

Fig. 2A and B compare forewing lengths plotted against maximum head widths, between adults obtained from a short-wing selected sub-line and an unselected line. All individuals emerged as adults with relatively short wings in the former ($n = 27$ and 38 in females and males), whereas most individuals developed long wings in the latter, except for a few adults with short wings in both sexes: 6.8% in females ($n = 73$) and 2.7% in males ($n = 76$). Interestingly, the hind femora were significantly shorter in the short-wing selected line than in the unselected line in both females ($t = -4.99$; $df = 108$; $P < 0.001$; Fig. 2C) and males ($t = -10.89$; $df = 110$; $P < 0.001$; Fig. 2D). Similar results were obtained for the males (Fig. 2B, D). These results suggest that adults with short wings are not simply locusts with abnormally short wings, but may represent a short-winged 'morph'. In the foregoing paragraphs, the terms short- and long-winged morphs will be used to designate those with short and long wings, respectively.

Neither F/C nor E/F ratios plotted against maximum head widths gave a complete separation between long-winged and short-winged adults (Fig. 3A-D). In contrast, E/C ratios clearly separated the two groups (Fig. 3E, F). Fig. 4 illustrates the frequency distribution of E/C ratios. These results indicate that an E/C ratio of 5.10 may be used to separate the two wing morphs in females. The males appeared to have a slightly higher ratio, *i.e.*, 5.25, that may separate the two wing morphs.

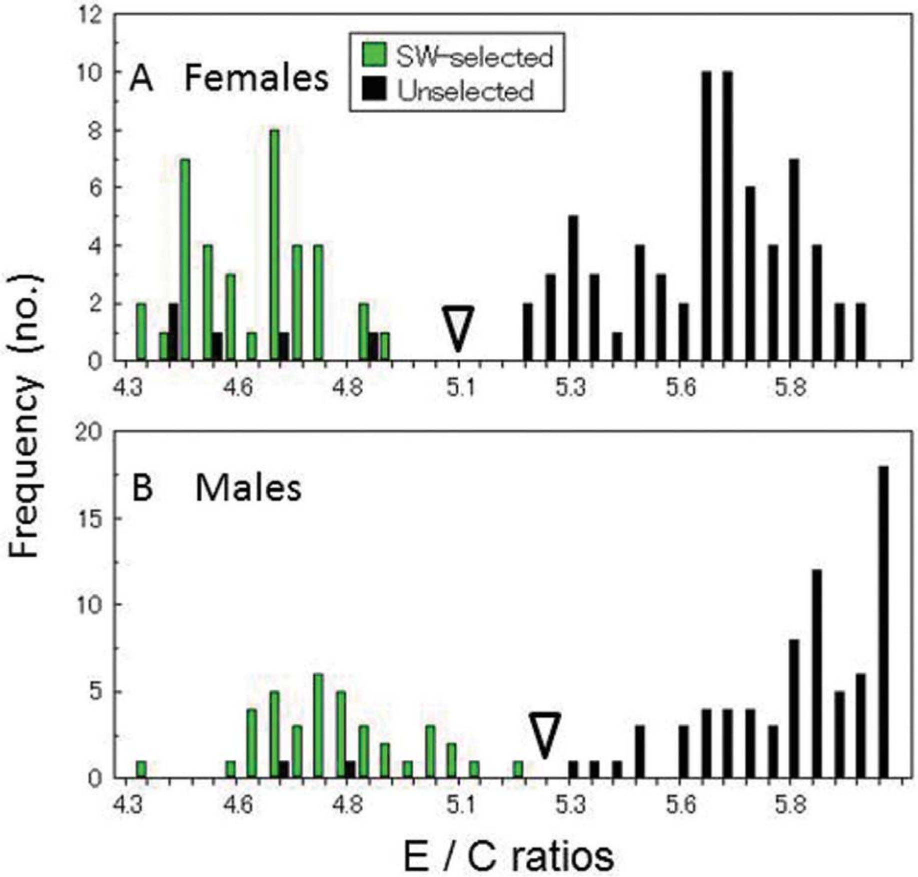

Fig. 4. Frequency distributions of E/C ratios in females (A) and males (B) in a short-wing selected (SW) and unselected line of a *L. migratoria* Tsushima strain. Triangles indicate an E/F ratio separating short-winged morphs and long-winged morphs.

Table 1 summarizes the mean body dimensions and morphometric ratios for the two wing morphs after those individuals that had an E/C ratio smaller than the above criteria were categorized as short-winged morphs. No significant difference was found in head width between the two morphs, whereas significant differences were obtained for hind femur and wing lengths. The differences remained significant when the comparison was made with maximum head width as a covariate (ANCOVA: $F = 474.12$; $df = 1$, 118 in females; $F = 174.93$; $df = 1$, 111 in males for hind femur length; $F = 311.59$; $df = 1$, 118 in females; $F = 102.20$; $df = 1$, 111 in males for the forewing length; $P < 0.001$ each). All morphometric ratios examined were significantly larger in the short-winged morphs than in the long-winged morphs in either sex (Table 1).

Genetics of the short-winged morph.—Crossing between short-winged morphs of the Tsushima strain and long-winged morphs of the Okinawa albino strain produced a dark-colored F_1 generation with long wings ($n > 150$), indicating that the long-winged morph and pigmented body color are dominant traits. In the F_2 generation, the proportions of morphs in each sex were not significantly different between the two cages and the ratio, long-winged to short-winged, did not deviate from 3:1 (Table 2, $P > 0.05$, χ^2-test). The same conclusion was drawn if the data for each sex from the two cages or those from the two sexes were combined ($P > 0.05$, χ^2-test). These results indicate that the short-winged trait is inherited as a single Mendelian unit. In this study, the numbers of albino and pigmented (normal) locusts were not recorded, but albino individuals were observed as both long-winged and short-winged morphs (Fig. 1C, D).

Discussion

This study demonstrated that adults with unusually short wings are not monsters produced under artificial rearing conditions, but represent a short-winged morph that exhibits not only short wings but also shorter hind legs than the long-winged phenotypes in *L. migratoria*. Unlike the long-winged adults, the short-winged adults can fly for only a few meters, although precise measurements have

Table 1. Body dimensions and morphometric ratios of short-winged (SW) and long-winged (LW) morphs in a *L. migratoria* Tsushima strain. C- head width, F- hind femur length, E- forewing length.

Females							
	C (mm)	F (mm)	E (mm)	F/C	E/F	E/C	n
SW	8.6 ± 0.6	24.3 ± 2.1	39.0 ± 3.0	2.85 ± 0.10	1.61 ± 0.05	4.57 ± 0.15	42
LW	8.4 ± 0.5	27.0 ± 2.1	46.8 ± 3.0	3.22 ± 0.12	1.73 ± 0.61	5.58 ± 0.20	68
Statistics	t-test NS	t = - 6.65***	t = - 13.41***	Z = -8.64***	Z = -7.99***	Z = -8.79***	
Males							
	C (mm)	F (mm)	E (mm)	F/C	E/F	E/C	
SW	6.9 ± 0.4	20.8 ± 2.0	32.8 ± 2.0	3.01 ± 0.11	1.58 ± 0.05	4.75 ± 0.17	40
LW	6.9 ± 0.7	23.7 ± 1.1	40.4 ± 1.7	3.40 ± 0.11	1.71 ± 0.05	5.80 ± 0.21	73
Statistics	t-test NS	t = - 11.87***	t = - 20.98***	Z = - 8.62***	Z = - 8.13***	Z = - 8.77***	

Table 2. The numbers of short-winged (SW) and long-winged (LW) morphs in the F_2 generation of crosses between short-winged males (Tsushima strain) and long-winged females (Okinawa albino strain).

	Females		Males		
Group	SW	LW	SW	LW	Total
Cage 1	20	66	26	81	193
Cage 2	21	50	16	65	152
Total	41	116	42	146	345

Proportions of the two wing morphs in each sex did not deviate significantly from a 1:3 ratio ($P > 0.05$, χ^2 test).

yet to be performed. Measurements of body dimensions indicate no significant difference in head width between the two wing morphs. This finding suggests that the two wing morphs are similar in body size except for the wings and legs. The ratio of forewing length to maximum head width may be a good parameter for identifying these wing morphs in this locust.

Morphometric analyses indicate that the F/C and E/F ratios were smaller in short-winged morphs than long-winged morphs in *L. migratoria*. These ratios were originally calculated to separate locusts in different phases by Stower *et al.* (1961) and the functional significance of the ratios is not known. In phase polyphenism, solitarious locusts have a smaller E/F value, but a larger F/C value than their gregarious counterparts (Stower *et al.* 1961). It is easy to suppose that the long wings relative to body size (*e.g.*, larger E/F ratio) found in gregarious adults reduces wing loading, thus facilitating long-distance migration. Likewise, smaller F/C ratios mean relatively shorter, lighter legs. These differences might explain the occurrence of such ratios in gregarious adults. However, in the wing polymorphism of this locust, short-winged morphs, which are apparently not good fliers, have even shorter legs than those of the migratory long-winged morphs. Short legs might be functionally associated with other behaviors than flight, although no experimental evidence for this hypothesis is available.

Dean (1989) reported that *Phaulacridium vittatum* short-winged morphs had longer hind femora than long-winged morphs in females but not in males. However, this finding was based on field-collected specimens and he suggested that further investigation should be conducted with animals of known origin, reared under uniform conditions. It would be interesting to examine how short-winged morphs of *L. migratoria* modify their morphometric ratios in response to different population densities.

Seasonal wing-length variation is often controlled by environmental factors such as photoperiod and temperature in insects (Tauber *et al.* 1986, Danks 1987, Dingle 1996, Saunders 2002). The present study suggests that the short-winged morph of *L. migratoria* is not influenced by photoperiod. In contrast, crossing experiments demonstrated that the short-winged morph was controlled by a simple recessive Mendelian unit.

Whether the short-winged morph of *L. migratoria* occurs in the field is unknown and no published record describing such incidence appears to exist. A total of more than 300 adults were collected on Tsushima Island in July and October 2008, but no short-winged morph was found (Tanaka, S., unpub. observations). However, it appears probable that this recessive gene is present in the Tsushima population, because short-winged individuals appeared in the F_2 generation of two of 14 family lines. Presumably, inbreeding made this recessive trait manifest in the laboratory. However, the possibility that the short-winged morph occurred by a gene mutation in the laboratory cannot be excluded, as reported for a lygaeid bug in which no short-winged morph is known in field populations (Klausner *et al.* 1981).

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