Phase-dependent morphometric traits of the albino strain of *Schistocerca gregaria* (Orthoptera: Acrididae)

Meir Paul Pener[1]

1 Department of Cell and Developmental Biology, The Hebrew University of Jerusalem, Israel.

Corresponding author: *Meir Paul Pener* (pener@mail.huji.ac.il)

Academic editor: *Michel Lecoq* | Received 2 May 2017 | Accepted 3 August 2017 | Published 13 October 2017

http://zoobank.org/A28546C7-53BB-445D-A2CF-F89D6C84BAF4

Citation: Pener MP (2017) Phase-dependent morphometric traits of the albino strain of *Schistocerca gregaria* (Orthoptera: Acrididae). Journal of Orthoptera Research 26(2): 81–84. https://doi.org/10.3897/jor.26.20012

Abstract

Sugahara et al. (2017) reported that unlike the wild type, the albino strain of *Schistocerca gregaria* does not show phase-dependent shift in the morphometric ratio of F/C (= length of the hind femur/maximum width of the head [caput]). In contrast, my old, unpublished, observations clearly demonstrate that *S. gregaria* albinos exhibited considerable phase-dependent shift in the morphometric ratios F/C and E/F (= length of the fore-wing [elytron] divided by length of the hind femur). Considering the report of Sugahara et al. (2017), I decided to publish my old results.

Key words

albino strain, crowded locusts, Desert locust, E/F ratio, F/C ratio, isolated locusts, normal strain, number of eye stripes

Introduction

In a recent publication, the genetic background of albinism and the related molecular biology of corazonin were studied in two species of locusts, *Locusta migratoria* (L.) and *Schistocerca gregaria* (Forsk.). Concerning *S. gregaria*, the authors reported that "unlike the wild type, the albino strain of this locust did not show a phase-dependent shift in a morphometric trait ..." (Sugahara et al. 2017, abstract, p. 41). The F/C ratio (length of the hind femur divided by maximum width of the head) constituted the morphometric trait investigated. It may be added that a phase-dependent shift in this morphometric trait does exist in *L. migratoria* albinos (Yerushalmi et al. 2001, Hoste et al. 2002).

In the frame of my Ph.D. thesis, in 1960–1962, I studied albinos of *S. gregaria*, including the morphometric ratios of F/C (see above) and E/F (length of the elytron [fore wing] divided by length of the hind femur). At that time it was strictly compulsory at the Hebrew University to submit the thesis in Hebrew. However, I sent a draft of an English manuscript to Sir Boris Uvarov asking for his comments. The manuscript was devoted to a portion of the morphometric ratios of *S. gregaria* albinos in comparison with these ratios in normally colored conspecific locusts. This draft was strongly based on Dirsh's (1953) scale of "percentage of gregarisation". Uvarov suggested revision of the manuscript, gently implying that he was not enthusiastic about Dirsh's concept of percentage of gregarisation. He also pointed out the possibility of multivariate analysis according to the then newly published morphometric studies by Stower et al. (1960). I was unable to follow Stower et al. (1960) because I kept the F/C and E/F values, but after obtaining the ratios, I discarded the values of F, C, and E. I never revised the manuscript, but in my Ph.D. thesis (in Hebrew) I have the average values of F/C and E/F which clearly demonstrate that *S. gregaria* locusts exhibit a phase-dependent shift in these ratios. I decided to publish my 55–57-year-old results, in order to contradict the conclusion of Sugahara et al. (2017). It should be emphasized that the same laboratory strain of albinos of *S. gregaria* was studied by me and by Sugahara et al. (2017), albeit over 50 years of difference in time. Obviously, the contradicting results need some explanation.

Materials and methods

The origin of the normally colored strain of *S. gregaria* and its maintenance as a crowded stock culture were described by Shulov and Pener (1963) and again by Pener and Lazaroviçi (1979). The strain of the albino mutants of *S. gregaria* was kindly supplied by the Anti-Locust Research Centre London, just two years after this strain had been described by Hunter-Jones (1957). Crowded stock of the albinos was maintained similarly to the normally colored strain. F, C and E were measured with a Vernier calliper (±0.1mm) according to fig. 1 of Dirsh (1953).

Hatchlings of isolated locusts were placed, each separately, into ¼-liter glass-jars and at the beginning of the 4th instar each was transferred to a ½-liter glass-jar. The jars were covered with metal mesh. Each jar was surrounded with black paper to prevent visual contact. Within a day after molt to adult each locust was placed into a 12-liter celluloid cage, again covered with metal mesh. Males were transferred to females once a week for one day.

Both the crowded and isolated locusts were kept in a heated room, illuminated and additionally heated continuously (24-h per day) by incandescent electric bulbs, yielding a rather high temperature, about 35°C. The food varied according to the season of the year, maize, lucerne, wheat, and sometimes other Graminae, all of them with flaked oat. Care was exerted to feed parallel generations with the same kind of food. I do not claim that these conditions constitute the optimum for obtaining phase-dependent morphometric differences. However, the fact remains that certain phase-dependent morphometric differences were found under these conditions. Also, my conditions are not related to the fact that Sugahara et al. (2017) obtained no phase-related morphometric shift in the F/C ratio of the same albino strain of *S. gregaria*.

Crowded albino and normally colored locusts were kept and measured over 16 consecutive generations. A portion of newly molted normally colored adult locusts were separated from the F_7 generation of the crowded locusts and placed each into a separate celluloid cage. They were considered as a transitional generation from crowding to isolation. Hatchlings from eggs laid by this transitional generation constituted F_{s1} isolated generation. This method for establishing isolated stocks was described later by Maeno and Tanaka (2009) studying phase-dependent morphometric changes in *S. gregaria*. The F_{s1} isolated generation was parallel with the F_8 crowded generation. The isolated stock was maintained and measured in each generation, up to the F_{s4} generation (inclusive). Normally colored isolated stock was again separated from the crowded stock by the same method, F_{14} constituting the transitional generation and F_{sI} the first isolated generation measured. F_{sI} was parallel to F_{15} crowded generation. One additional isolated generation, F_{sII}, parallel to F_{16}, was also measured.

Albino locusts were isolated by the same method with one exception; F_8 constituted the transitional generation, so F_{s1} was parallel to F_9 crowded albino generation. Therefore, one generation less isolated albinos were measured than isolated normally colored locusts.

Eye stripes of isolated adult locusts were counted in males and females. The number of eye stripes reflects the number of instars from hatching to adult (inclusive). Crowded (gregarious) *S. gregaria* has five nymphal instars and the adult stage; therefore, the number of their eye stripes is always six. Isolated (solitarious) conspecifics often have an extra molt including an extra eye stripe (Uvarov 1966 and references therein). This extra molt and extra eye stripe is more common in isolated females of *S. gregaria* than in males (Maeno and Tanaka 2009).

Results

The morphometric ratios for normally colored crowded locusts (Table 1) and for crowded albinos (Table 3) are presented only for those generations which were parallel to the respective isolated generations. These ratios for the isolated generations are shown for normally colored locusts in Table 2 and for albinos in Table 4. It may be recalled that the ratio F/C is lower in crowded (gregarious) than in isolated (solitarious) *S. gregaria*; therefore, at

Table 1. Morphometrics of crowded *Schistocerca gregaria*, normal strain.

Generation	F/C		E/F		n*	
	♂	♀	♂	♀	♂	♀
F_8	3.49	3.52	2.11	2.15	15	13
F_9	3.52	3.52	2.13	2.15	15	8
F_{10}	3.45	3.51	2.15	2.20	20	20
F_{11}	3.51	3.54	2.12	2.17	20	20
F_{15}	3.49	3.47	2.16	2.23	20	20
F_{16}	3.61	3.69	2.10	2.14	20	20
Weighted average	3.51	3.54	2.13	2.18		
Sum					110	101

*n = Number of locusts measured.

Table 2. Morphometrics of isolated *Schistocerca gregaria*, normal strain.

Generation		F/C		E/F		n*		% with 7 eye stripes**	
	Parallel to	♂	♀	♂	♀	♂	♀	♂	♀
F_{s1}	F_8	3.86	3.96	1.97	1.99	8	15	75.0	87.5
F_{s2}	F_9	3.87	3.91	1.97	2.01	16	19	0.0	5.0
F_{s3}	F_{10}	3.83	3.90	2.00	2.01	19	12	4.5	33.3
F_{s4}	F_{11}	3.96	3.91	1.97	2.01	16	15	18.7	50.0
F_{sI}	F_{15}	3.81	3.93	2.01	2.02	6	9	0.0	10.0
F_{sII}	F_{16}	3.83	3.97	2.00	2.00	11	26	0.0	15.4
Weighted average		3.87	3.90	1.99	2.01				
Sum						76	96		

*n = Number of locusts measured.

** The number of eye stripes is either six or seven. The % values in the table are based on a larger number of locusts than those measured.

Table 3. Morphometrics of crowded *Schistocerca gregaria*, albino strain.

Generation	F/C		E/F		n*	
	♂	♀	♂	♀	♂	♀
F_9	3.52	3.60	2.05	2.08	13	6
F_{10}	3.58	3.61	2.05	2.09	20	20
F_{11}	3.55	3.59	2.04	2.10	20	20
F_{15}	3.46	3.53	2.05	2.10	20	20
F_{16}	3.60	3.60	2.05	2.09	19	17
Weighted average	3.54	3.58	2.05	2.09		
Sum					92	83

*n = Number of locusts measured.

transition from crowding to isolation, F/C crowded minus F/C isolated, yields negative values. In contrast, E/F is higher in crowded (gregarious) than in isolated (solitarious) conspecifics.

Table 5 presents the shifts in the morphometric ratios obtained by transition from crowding to isolation. The shift of – 0.36 in the F/C ratio for normally colored males and females may be unimpressive. However, according to Dirsh's (1953) linear scale of percentage of gregarisation a shift of – 0.36 in F/C represents a shift as high as ca. 40% and 50% of gregarisation for normally colored males and females, respectively. In terms of Dirsh's scale, the shift in the E/F ratios, both for normally colored males and females, represents a shift in the percentage of gregarisation even higher than that represented by the F/C ratio.

Table 5 clearly reveals a considerable shift in the morphometric ratios for albino males and females. However, these shifts are less extensive than the shifts of the corresponding ratios for normally colored locusts. Notably, a similar conclusion was observed for morphometric shifts by transition from crowding to isolation in normally colored and albinos of *Locusta migratoria* (see Yerushalmi et al. 2001, Hoste et al. 2002).

As already noted, the number of eye stripes in crowded (gregarious) *S. gregaria* is always six. The percentages of isolated normally colored locusts and isolated albinos with seven eye stripes are shown in Tables 2 and 4, respectively. The results indicate that more females than males exhibited seven eye stripes. This finding fits the conclusion of Maeno et al. (2004) on rare occurrence of isolated males having six nymphal instars, which means seven eye stripes, in normally colored *S. gregaria*.

Table 4. Morphometrics of isolated *Schistocerca gregaria*, albino strain.

Generation		F/C		E/F		n*		% with 7 eye stripes**	
	Parallel to	♂	♀	♂	♀	♂	♀	♂	♀
F_{s1}	F_9	3.91	3.93	2.01	2.03	18	12	5.9	8.3
F_{s2}	F_{10}	3.90	3.88	2.01	1.96	10	6	0.0	22.2
F_{s3}	F_{11}	3.80	3.90	2.01	1.96	5	5	0.0	85.7
F_{sI}	F_{15}	3.66	3.76	2.02	2.04	18	14	0.0	13.3
F_{sII}	F_{16}	3.83	3.97	1.94	1.96	19	21	0.0	54.5
Weighted average		3.81	3.90	1.99	1.99				
Sum						70	58		

*n = Number of locusts measured.

** The number of eye stripes is either six or seven. The % values in the table are based on a larger number of locusts than those measured.

Table 5. Shifts in the average values of the morphometric ratios from crowding to isolation.*

Ratio	F/C				E/F			
Strain	Normal		Albino		Normal		Albino	
Sex	♂	♀	♂	♀	♂	♀	♂	♀
Crowded minus isolated	−0.36	−0.36	−0.27	−0.32	0.14	0.17	0.06	0.10

*Weighted average values are taken from Tables 1–4.

Discussion

Unfortunately, no statistical analyses were carried out on the data in Tables 1–5. In the early sixties of the last century statistical analyses were less obligatory than today. Raw data are now gone, leaving only the summary statistics here reported in the tables. Nevertheless, as already outlined, according to Dirsh's (1953) "percentage of gregarisation" large differences exist between crowded and isolated normally colored locusts, as well as between crowded and isolated conspecific albinos.

Dearn's (1977) studies on albinos of *S. gregaria* also indicated density-dependent differences in morphometrics. However, Dearn (1977) measured only crowded locusts. He found that the morphometric ratios of the albinos approach, though do not reach, those of the 'wild type'. Dearn (1977) also cited the morphometric ratios from my unpublished Ph. D. thesis (a Hebrew copy was deposited in the library of the Anti-Locust Research Centre). These ratios cited by him for crowded locusts are based on all 16 generations and are slightly different from those in Tables 1 and 3 of the present paper that show only those generations of the crowded locusts which are parallel to their isolated conspecifics. As for the isolated locusts, Dearn's (1977) citations may differ from the present data by one or two hundredths, probably because he cited unweighted averages, or rounded slightly differently from thousandth to hundredth. In one ratio, F/C, isolated albino males, Dearn (1977) made a mistake, his citation is incorrect, the correct value is 3.81 not 3.90. Sugahara et al. (2017) do not cite Dearn's (1977) paper.

The method of transition from crowding to isolation, isolating newly molted adults and keeping under isolation their progeny, as described above (see materials and methods), clearly differed from that employed by Sugahara et al. (2017) who isolated hatchlings from eggs laid by crowded locusts. However, Maeno and Tanaka (2009) isolating hatchlings from crowded parents of normally colored *S. gregaria* and rearing them under isolation to adults, found F/C values intermediate between those characteristic to isolated and crowded locusts. Sugahara et al. (2015) also observed a shift in the F/C values by isolating progeny of normally colored crowded locusts as late as 2nd instar nymphs.

The samples measured by Sugahara et al. (2017) are sufficiently large (71 crowded and 40 freshly isolated albinos); therefore, sample size does not seem to be responsible for their finding.

By extensive correspondence with Prof. Seiji Tanaka (coauthor of the Sugahara et al. (2017) article) we did not find a satisfying explanation. However, it is possible that the albino mutant described by Hunter-Jones (1957) lost in time the ability to undergo phase-dependent morphometric shift. I obtained my albino mutant from London in 1959, just two years after their description. The same albino mutant, six males and six females, originating from a locust colony (Hunter-Jones 1957), made a long way, about almost 60 years, from London to Prof. S. Andersen* (Copenhagen University, Denmark) then to Prof. A. De Loof's laboratory (Leuven, Belgium) and finally to Japan. It may be added that when a locust colony is transferred from one laboratory to another, usually a limited number of adults or egg pods are actually transferred, not the whole colony. Berthier et al. (2010), investigating various colonies of locusts, found that even in standard and static laboratory colonies there is a genetic drift, meaning lowering the allele richness. After so many transfers of the albino strain of *S. gregaria*, the possibility of loss, or partial loss, of phase-dependent morphometric shift should be further investigated. This investigation should be carried out with one or two transitional generations when establishing an isolated line, like the full procedure as described by Maeno and Tanaka (2009).

In any case, the results of my Ph. D. thesis clearly demonstrate that the albino mutation of *S. gregaria* does exhibit, or did exhibit, density-dependent morphometric shifts.

Acknowledgements

I sincerely thank Prof. Seji Tanaka for interesting information on the subject.

References

Berthier K, Chapuis M-P, Simpson SJ, Ferenz H-J, Habib Kane CM, Kang L, Lange A, Ott SR, Babah Ebbe MA, Rodenburg KW, Rogers SM, Torto B, Vanden Broeck J, van Loon JJA, Sword GA (2010) Laboratory populations as a resource for understanding the relationship between genotypes and phenotypes: A global case study in locusts. Advances in Insect Physiology 39: 1–37. https://doi.org/10.1016/B978-0-12-381387-9.00001-4

Dearn JM (1977) Pleiotropic effects associated with the albino mutation in the desert locust, *Schistocerca gregaria* (Forsk.), and their relationship to phase variation. Acrida 6: 43–53.

Dirsh VM (1953) Morphometrical studies on phases of the Desert Locust. Anti-Locust Bulletin 16: 1–34.

Hoste B, Simpson SJ, Tanaka S, De Loof A, Breuer M (2002) A comparison of phase-related shifts in behavior and morphometrics of an albino strain deficient in [His7]-corazonin, and a normally colored *Locusta migratoria* strain. Journal of Insect Physiology 48: 791–801. https://doi.org/10.1016/S0022-1910(02)00106-3

* Sugahara et al. (2017) wrote Anderson, but the correct name is Andersen.

Hunter-Jones P (1957) An albino strain of the desert locust. Nature 180: 236–237. https://doi.org/10.1038/180236b0

Maeno K, Tanaka S (2009) The trans-generational phase accumulation in the desert locust: Morphometric changes and extra molting. Journal of Insect Physiology 55: 1013–1020. https://doi.org/10.1016/j.jinsphys.2009.07.005

Maeno K, Gotoh T, Tanaka S (2004) Phase-related morphological changes induced by [His^7]-corazonin in two species of locusts, *Schistocerca gregaria* and *Locusta migratoria* (Orthoptera: Acrididae). Bulletin of Entomological Research 94: 349–357. https://doi.org/10.1079/BER2004310

Pener MP, Lazaroviçi P (1979) Effect of exogenous juvenile hormones on mating behaviour and yellow colour in allatectomized adult male desert locusts. Physiological Entomology 4: 251–261. https://doi.org/10.1111/j.1365-3032.1979.tb00202.x

Shulov A, Pener MP (1963) Studies on the development of eggs of the desert locust (*Schistocerca gregaria* Forskål) and its interruption under particular condition of humidity. Anti-Locust Bulletin 41: 1–59.

Stower WJ, Davies DE, Jones IB (1960) Morphometric studies of the desert locust, *Schistocerca gregaria* (Forsk.). Journal of Animal Ecology 29: 309–339. https://doi.org/10.2307/2206

Sugahara R, Saeki S, Jouraku A, Shiotsuki T, Tanaka S (2015) Knockdown of the corazonin gene reveals its critical role in the control of gregarious characteristics in the desert locust. Journal of Insect Physiology 79: 80–87. https://doi.org/10.1016/j.jinsphys.2015.06.009

Sugahara R, Tanaka S, Jouraku A, Shiotsuki T (2017) Two types of albino mutants in the desert and migratory locusts are caused by gene defects in the same signaling pathway. Gene 608: 41–48. https://doi.org/10.1016/j.gene.2017.01.022

Uvarov BP (1966) Grasshoppers and Locusts – A Handbook of General Acridology, Vol. 1. Cambridge Univesity Press, 481 pp.

Yerushalmi Y, Tauber E, Pener MP (2001) Phase polymorphism in *Locusta migratoria*: the relative effects of geographic strains and albinism on morphometrics. Physiological Entomology 26: 95–105. https://doi.org/10.1046/j.1365-3032.2001.00220.x