

STUDIES IN INTRASPECIFIC VARIATION

XIII. SIZE OF EYE AND ITS RATIOS IN THE DESERT LOCUST IN RELATION TO PHASE AND EYE-STRIFE POLYMORPHISMS

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(1) Variations in eye-size (length, width and the Width/Length ratio) were studied in relation to phase and eye-stripe polymorphisms in the Desert Locust, *Schistocerca gregaria* (Forsk.). (2) Eyes are elongat-oval, and are about 3.25-4.75 mm long and 2.25-3.00 mm wide (in both cases including the ocular sclerite). They are generally slightly smaller in males than in females. (3) In both the dimensions (the length, A, and the width, B) the eyes are significantly smaller in phase *gregaria* (all of which are 6-eye-striped) than in phase *solitaria*; the latter are about 1.4-11.8 per cent larger. (4) Within the *solitaria* phase, where 5- to 8-eye-striped polymorphs occur (mostly with 6 and 7 eye-stripes), eyes in 7-striped individuals are larger than in 6-striped ones by about 3.1-7.4 per cent. No data are available for 5- and 8- striped individuals. (5) Length and width are strongly correlated positively; the correlation coefficient is higher in females than in males. (6) The ratio Width/Length (B/A) varies within narrow limits (means 0.648-0.664) and shows no significant differences in respect of phase, sex and eye-stripe categories. Thus, irrespective of eye-size, its shape remains nearly constant. (7) In both length and width sexual dimorphism is lower in phase *gregaria* than in *solitaria* by about 2.83-9.52 per cent. The ratio B/A shows no sexual dimorphism. (8) The presence of smaller eyes in phase *gregaria* as compared to *solitaria* is probably a device to reduce the amount of strong sunlight entering the eyes, and seems to be correlated with differences in the flying and marching habits in the two phases.

INTRODUCTION

Phase and non-phase polymorphs are now well established in the Desert Locust, *Schistocerca gregaria* (Forsk.) (Orthoptera, Acrididae,) and have proved to be of practical importance for the prediction of swarming (Roonwal, 1945; Bhanotar, 1975). Polymorphism in the size of body-parts and the relevant ratios has been studied by Roonwal (1947-58) and others, and eye-stripe polymorphism (5-8 stripes) by Roonwal (1936-62). A summary is given by Roonwal (1962), and the rare 5-eye-stripe polymorph also discussed by him (Roonwal, 1971).

The size of the compound eye has, however, not been adequately studied. Dirsh (1953) gave values for its length and width in relation to *gregaria* and *solitaria*

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phase variations, but eye-stripe polymorphism was ignored. We have now studied eye-size in relation to the known phase and eye-stripe polymorphs, and the results are presented here. The only other locust in which eye-size has been studied is the African Migratory Locust, *Locusta migratoria migratorioides*, by Thomas (1942) (see below, Discussion).

MATERIAL AND METHODS

A total of 284 examples of the Desert Locust from India (106 from swarms, in phase *gregaria*; and 178 from low, scattered populations, in phase *solitaria*) were measured under a binocular. Two measurements were taken: maximum length (A) and maximum width (B); both are the shortest straight line distances between two parallels marking the maximum outer limits of the eyes (including the ocular sclerite) (Fig. 1). [Dirsh (1953), who also had studied eye-size, made no mention of the ocular sclerite, but had probably excluded it since his values are consistently lower than ours]. Significance tests were carried out for various probability levels of 5%, 1% and 0.1%. The sexes and the various phase and eye-stripe polymorphs were analysed separately.

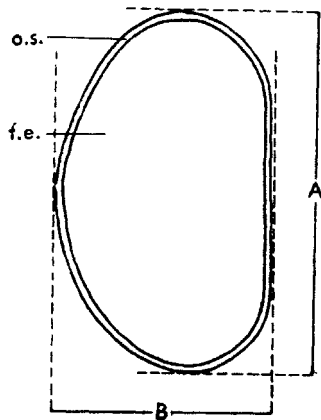


Fig. 1. *Schistocerca gregaria*. Right eye, to show method of measurement. A, maximum length; B, maximum width; f.e., faceted region; o.s., ocular sclerite (this is included in the measurements)

RESULTS

The two compound eyes are elongate-oval and are about 3.25–4.75 mm long and 2.25–3.00 mm broad (in both cases including the ocular sclerite). They are, as a rule, slightly smaller in males than in females.

Length and Width of Eyes

In both length and width the eyes are significantly smaller in phase *gregaria* than in phase *solitaria* (Fig. 2, and Tables I and II).

TABLE I
Schistocerca gregaria: Range, Mean, and Standard Deviation (with Standard Error) for characters A and B and the ratio B/A in various phase-sex-eye-stripe groups

Phase, sex and number of eye-stripes	n	Max. length of eye (A) (mm)		Max. width of eye (B) (mm)		Ratio B/A	
		Mean \pm S.E.	S.D. \pm S.E.	Mean \pm S.E.	S.D. \pm S.E.	Mean \pm S.E.	S.D. \pm S.E.
greg. ♂♂ (6)	55	3.82 \pm 0.03	0.19 \pm 0.02	2.47 \pm 0.02	0.13 \pm 0.01	0.648 \pm 0.006	0.043 \pm 0.004
greg. ♀♀ (6)	51	3.93 \pm 0.03	0.19 \pm 0.02	2.54 \pm 0.02	0.18 \pm 0.02	0.648 \pm 0.005	0.038 \pm 0.004
sol. ♂♂ (6)	75	3.87 \pm 0.02	0.18 \pm 0.01	2.52 \pm 0.01	0.12 \pm 0.01	0.651 \pm 0.002	0.019 \pm 0.001
sol. ♀♀ (6)	22	4.07 \pm 0.04	0.21 \pm 0.03	2.67 \pm 0.03	0.16 \pm 0.02	0.657 \pm 0.005	0.024 \pm 0.004
sol. ♂♂ (7)	27	3.99 \pm 0.04	0.19 \pm 0.03	2.65 \pm 0.03	0.14 \pm 0.02	0.664 \pm 0.006	0.031 \pm 0.004
sol. ♀♀ (7)	54	4.37 \pm 0.03	0.21 \pm 0.02	2.84 \pm 0.02	0.15 \pm 0.01	0.651 \pm 0.005	0.035 \pm 0.003
sol. ♂♂ (6 & 7)	102	3.90 \pm 0.02	0.19 \pm 0.01	2.55 \pm 0.01	0.14 \pm 0.01	0.654 \pm 0.003	0.034 \pm 0.002
sol. ♀♀ (6 & 7)	76	4.28 \pm 0.03	0.24 \pm 0.02	2.79 \pm 0.02	0.17 \pm 0.01	0.653 \pm 0.003	0.026 \pm 0.002

n, Number of individuals; S.D., Standard Deviation; S.E., Standard Error

TABLE II

Schistocerca gregaria: Differences in mean values of length and width of eye in various polymorph-pairs

Length of eye			Width of eye		
Polymorph-pairs	Mean size (mm)	% difference	Polymorph-pairs	Mean size (mm)	% difference
<i>Males</i>					
Gr. ♂ (6)	3.82	1.4	Gr. ♂ (6)	2.47	2.1
Sol. ♂ (6)	3.87		Sol. ♂ (6)	2.52	
Gr. ♂ (6)	3.82	4.5	Gr. ♂ (6)	2.47	7.3
Sol. ♂ (7)	3.99		Sol. ♂ (7)	2.65	
Sol. ♂ (6)	3.87	3.1	Sol. ♂ (6)	2.52	5.2
Sol. ♂ (7)	3.99		Sol. ♂ (7)	2.65	
<i>Females</i>					
Gr. ♀ (6)	3.93	3.6	Gr. ♀ (6)	2.54	5.1
Sol. ♀ (6)	4.07		Sol. ♀ (6)	2.67	
Gr. ♀ (6)	3.93	11.2	Gr. ♀ (6)	2.54	11.8
Sol. ♀ (7)	4.37		Sol. ♀ (7)	2.84	
Sol. ♀ (6)	4.07	7.4	Sol. ♀ (6)	2.67	6.4
Sol. ♀ (7)	4.37		Sol. ♀ (7)	2.84	

Gr., phase *gregaria*; Sol., phase *solitaria*: (6) and (7), with 6 and 7 eye-stripes respectively

Maximum length (A): Within each sex the mean length is lowest in phase *gregaria* (all are 6-eye-striped), 1.4–3.6 % higher in 6-eye-striped *solitaria*, and highest in 7-striped *solitaria* (4.5–11 % higher than 6-striped *gregaria*). Within each category-pair, the increase among females is about 1.4–2.6 times higher than in males.

Maximum width (B): This too is lowest in phase *gregaria* (all are 6-eye-striped), 2.1–5.1 % higher in 6-eye-striped *solitaria*, and highest in 7-striped *solitaria* (7.3–11.8 % higher than in 6-striped *gregaria*). Within each category-pair the width is upto about 1.2–2.4 times higher in females than in males.

Correlation between length and width (Table III): The length and width show

TABLE III

Schistocerca gregaria : Inter-phase and inter-sex comparisons of Correlation Coefficient between characters A and B (maximum length and width respectively of the compound eyes)

Phase, sex and number of eye-stripes	Correlation coefficient between A and B, with S.E.	Significance of difference between phase group pairs
<i>greg.</i> ♂♂ (6)	0.55 ± 0.09	NS
<i>sol.</i> ♂♂ (6)	0.44 ± 0.09	
<i>greg.</i> ♂♂ (6)	0.55 ± 0.09	NS
<i>sol.</i> ♂♂ (7)	0.45 ± 0.15	
<i>greg.</i> ♀♀ (6)	0.81 ± 0.05	NS
<i>sol.</i> ♀♀ (6)	0.58 ± 0.14	
<i>greg.</i> ♀♀ (6)	0.81 ± 0.05	*
<i>sol.</i> ♀♀ (7)	0.92 ± 0.02	
<i>greg.</i> ♂♂ (6)	0.55 ± 0.09	*
<i>greg.</i> ♀♀ (6)	0.81 ± 0.05	
<i>sol.</i> ♂♂ (6)	0.44 ± 0.09	NS
<i>sol.</i> ♀♀ (6)	0.58 ± 0.14	
<i>sol.</i> ♂ (7)	0.45 ± 0.15	**
<i>sol.</i> ♀ (7)	0.92 ± 0.02	

NS, Not significantly different; *, Significant at 5% level of probability;

** , Significant at 1% level of probability; S.E., Standard Error

considerable correlation with each other and vary in the same direction, the Correlation Coefficient being well above zero (thus signifying real association), as follows, according to phase and the number of eye-stripes :

Males

6-*greg.* 0.55±0.09
6-*sol.* 0.44±0.09
7-*sol.* 0.45±0.15

Females

6-*greg.* 0.81±0.05
6-*sol.* 0.58±0.14
7-*sol.* 0.92±0.02

The correlation is significantly higher in females than in males.

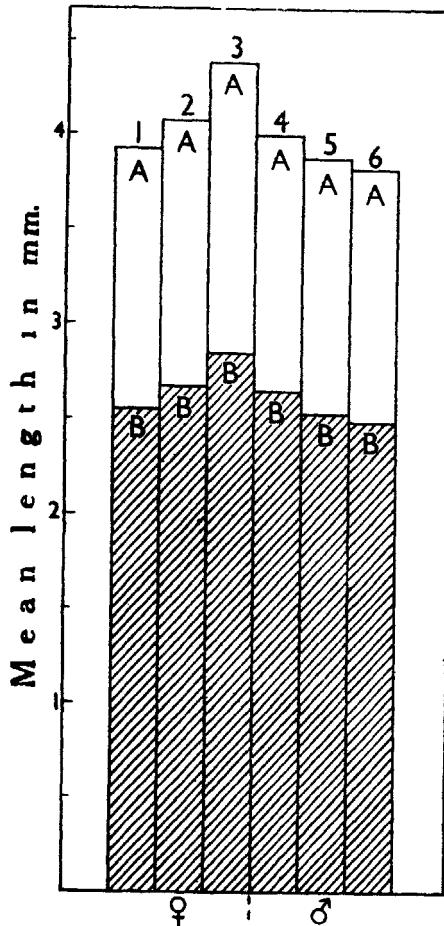


Fig. 2 *Schistocerca gregaria*. Histograms of mean size of eye. A, length (entire column); B (shaded part), width.

1 and 6, in 6-eye-striped phase *gregaria*; 2 and 5, in 6-eye-striped ph. *solitaria*; 3 and 4, in 7-eye-striped ph. *solitaria*.

Ratio Width/Length (B/A)

The mean of ratio Width/Length (B/A) varies within narrow limits (0.648 ± 0.005 to 0.664 ± 0.006). The differences are not significant in respect of phase-, sex- and eye-stripe polymorphs. Thus, irrespective of eye-size its shape remains nearly constant.

Sexual Dimorphism (Fig. 3 and Table IV)

Sexual Dimorphism Percentages (SDP) were calculated by the formula

$$\left[\left(\frac{\text{Mean } \text{♀}}{\text{Mean } \text{♂}} - 1 \right) \times 100 \right]$$

The SDP for eye-length, A, is significantly lower in 6-eye-striped phase *gregaria* (2.88 ± 0.98) than in 7-striped *solitaria* (9.52 ± 1.23) at all levels, but is not different from 6-striped *solitaria* (5.17 ± 1.29). Differences between 6- and 7-eye-striped *solitaria* are not significant. The SDP for eye-width, B, follows the same pattern. It is lower in 6-eye-striped phase *gregaria* (2.83 ± 1.25) than in 7-striped *solitaria* (7.17 ± 1.33) at the 5 % level, but is not different from 6-striped *solitaria* (5.95 ± 1.47). Differences between 6- and 7-eye-striped phase *solitaria* are also not significant.

TABLE IV
Schistocerca gregaria. Inter-phase comparison of Sexual Dimorphism Percentage (S.D.P.) for characters A and B, and the ratio B/A

Characters and ratio	Phase and number of eye-stripes	S.D.P.	Significance of difference between phase groups
A (max. length of compound eye)	<i>greg.</i> (6)	2.88	NS
	<i>sol.</i> (6)	5.17	
	<i>greg.</i> (6)	2.88	***
	<i>sol.</i> (7)	9.52	
B (max. width of compound eye)	<i>greg.</i> (6)	2.83	NS
	<i>sol.</i> (6)	5.95	
	<i>greg.</i> (6)	2.83	*
	<i>sol.</i> (7)	7.17	
B/A	<i>greg.</i> (6)	0	NS
	<i>sol.</i> (6)	0.92	
	<i>greg.</i> (6)	0	NS
	<i>sol.</i> (7)	0.15	

*** significant at 0.1% level of probability; Others as in Table II.

DISCUSSION

Within each sex in respect of both length and width the absolute size of eyes is smaller in phase *gregaria* than in *solitaria*. Dirsh (1953) came to the same

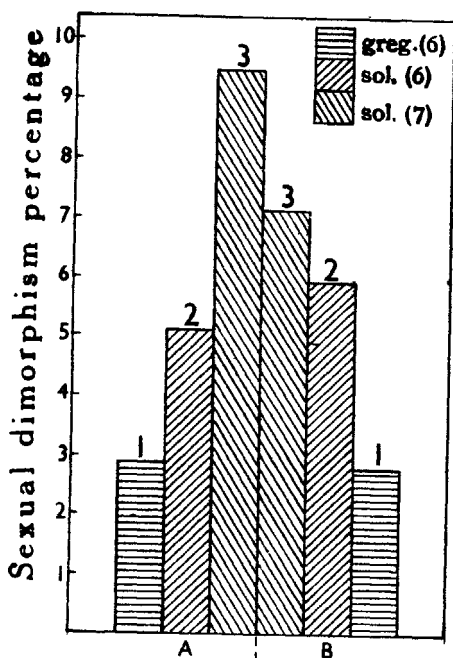


Fig. 3. *Schistocerca gregaria*. Histograms of Sexual Dimorphism Percentage (SDP) in mean values for length (A) and width (B) of eye.

1, in 6-eye-striped phase *gregaria*; 2 and 3, in ph. *solitaria* (6- and 7-eye-striped respectively).

conclusion for the sexes, but he had ignored eye-stripe polymorphs. All phase *gregaria* individuals are 6-eye-striped; phase *solitaria* individuals are mainly both 6- and 7-eye-striped, with 5- and 8-striped forms occurring occasionally in small numbers. Within each sex, eye-size, in respect of both length and width, is smaller in 6-striped individuals than in 7-striped ones; no data are available for 6- and 8-striped forms.

Briefly, the following conclusions are reached : (i) In absolute size phase *gregaria* individuals (all are 6-eye-striped) have the smallest eyes. (ii) Where eye-stripe polymorphs occur, as in phase *solitaria*, 6-striped individuals have smaller eyes than 7-striped ones. The greater size of the 7-striped individuals is partly explicable because the majority (c. 75%, but not all) of such individuals are produced by an extra-moult (Roonwal, 1947, p. 255). (iii) The ratio Width/Length is nearly constant, suggesting that irrespective of phase, sex, or eye-stripe polymorphisms, the shape of eyes remains more or less constant.

In the only other locust for which data on eyes are available, Thomas (1942) found in the African Migratory Locust, *Locusta migratoria migratorioides* (R. & F.), that, as in *Schistocerca gregaria*, the eye-shape, as judged by his ratio Length/Width, remains constant around 1.39-1.40 (means); and eyes (relative to other body-parts, e.g. elytron-length and head-width) are smaller in phase *gregaria* than in *solitaria*.

Probable significance of smaller eyes in phase gregaria

It is now known (Rao, 1960) that phase *gregaria* locusts do not avoid strong sunlight and undertake long migratory flights mostly during the day, whereas phase *solitaria* individuals tend to shun strong sunlight and fly mostly at night. Earlier, Roonwal (1947) had shown, from a study of eye pigmentation, that *gregaria* eyes are well protected against strong light by the heavier development of pigment and the presence of a post-retinular pigment layer which serves to absorb excessive light and functions as an "anti-halation" device; in contrast, *solitaria* eyes are lightly pigmented and lack the post-retinular pigment layer. The smaller eyes of phase *gregaria* introduces another factor which serves to reduce the amount of light entering the eyes, and thus protect them from excessive glare.

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ADDENDUM

In the South American Locust, *Schistocerca cancellata* (Serville), Roonwal and Bhanotar (1964) found that in males the eyes are longer in phase *gregaria* (mean length 3.38 ± 0.047 mm) than in phase *solitaria* (3.20 ± 0.045 mm), but in females there is no difference in this respect in the two phases. In eye-width there is no phase difference in either sex.

Roonwal, M. L. & Bhanotar, R.K. (1964). Eye-stripes, morphometric phase variation, especially of sternum, and sexual dimorphism in South American Locust, *Schistocerca cancellata* (Serville). from the Argentina. *Proc. zool. Soc. Calcutta*, **16** (1963), 162-192, 1 pl.