ON VARIATION IN THE NUMBER OF OVARIOLES AND ITS PROBABLE ORIGIN IN THE DESERT LOCUST, *SCHISTOCERCA GREGARIA* (FORSKÅL). [ORTHOPTERA, ACRIDIDAE.]

By M. L. ROONWAL, *M.Sc., Ph.D. (Cantab.), F.N.I.,*

Major, Indian Land Forces.

[*From the Zoological Survey of India, Benares Cantt.*]

INTRODUCTION.

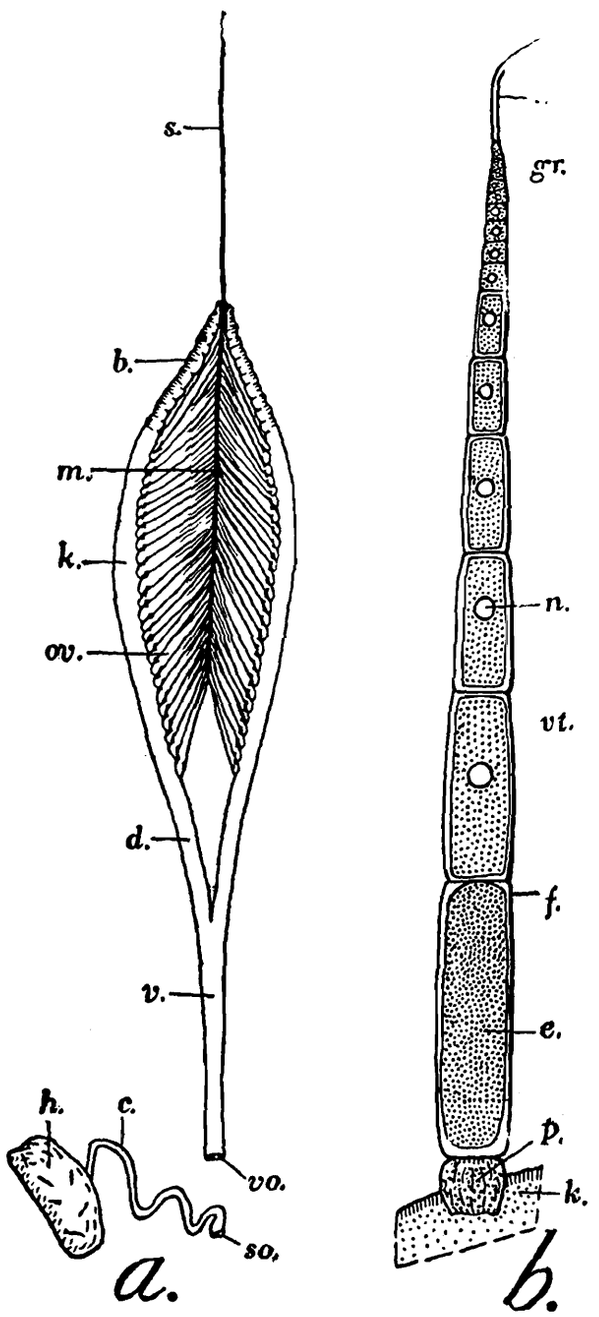
The Desert Locust, *Schistocerca gregaria* (Forskål), lays about 25 to over 100 eggs at each oviposition, the number varying from one oviposition to another and from female to female. This large number is to be coupled with an almost equally large number of ovarioles or eggs-tubes in the ovary, though the correspondence is not exact. Boldyrev (1929, p. 190) remarked for *Locusta migratoria* that " when a row of eggs matures, a certain percentage of the egg-tubes remains undeveloped, and the number of eggs produced is less than the number of egg-tubes" Nevertheless, in the Acrididae the number of ovarioles do provide us with a rough index of the number of eggs laid and thus of the reproductive capacity of the individuals. In this connection two problems, among several others, deserve consideration : (i) Is the difference in the reproductive rate under different environmental conditions, *e.g.*, at different temperatures and humidities, due to the reduction in the number of ovarioles ? (ii) Is there a difference in the number of ovarioles between the *gregaria* and *solitaria* phases, or between the various kinds of *solitaria* individuals (Roonwal, 1936, 1945-1946) ? Before, however, these and similar questions can be satisfactorily answered, we must know the natural variation in the number of ovarioles.

There are several accounts of the female reproductive organs of the Acrididae adults (Fénard, 1896, 1897 ; Berlese, 1909 ; Harman, 1925 ; Pospelov, 1926 ; Fedorov, 1927 ; Uvarov, 1928 ; Boldyrev, 1929 ; Nelsen, 1934 ; Snodgrass, 1935 ; Paoli, 1937 ; Jannone, 1938, 1939 ; Slifer, 1939-1943*a* ; Qadri, 1940 ; and others), and embryos and hoppers (Graber 1891 ; Nel, 1929 ; Nelsen 1934, 1934*a* ; Roonwal, 1937 ; and Qadri, 1940). Variation in the number of ovarioles, however, does not appear to have received attention except by Boldyrev (1929) and by Jannone (1938, pp. 318-319 ; 1939, pp. 280-281). Boldyrev noted in *Locusta migratoria* that the number of ovarioles varies in different individuals and in the right and left ovaries in the same individual. The total number, in eleven individuals, varied from 82-111, and the number in the right and left ovaries respectively from 40-55 and 42-56. The difference in the right and left ovaries of the same individual ranged from 0-4. In *Dociostaurus maroccanus* Jannone found no significant difference in the number of ovarioles between the phases *solitaria* and *transiens congregans* ; the number in each ovary is about 15-19, and that in both ovaries 30-37 An equal number in the two ovaries of a female is an exception rather than the rule. The first stage hopper has 15-16 ovarioles in each of the two ovaries.

I shall record here the variation in the number of ovarioles in the adults and hoppers of *Schistocerca gregaria* (phase *gregaria*) taken from various swarms in India. The probable mode of origin of asymmetry in the number of ovarioles in the right and left ovaries is also discussed.

The Ovaries.

A brief description of the adult ovaries (Text-fig. 1), as observed in phase *gregaria*, may first be given. In an immature adult the two



Text-fig. 1.—*Schistocerca gregaria* (Forskål).

(*a*). The ovary, its associated parts and the spermatheca of a freshly eclosed adult female. Dorsal view, with the antero-dorsal wall (not shown in the figure) of the genital cavity deflected backward. Semi-diagrammatic. x about 6. (*b*).—An ovariole from the same. Semi-diagrammatic. x about 60.

b., female accessory gland (*boyau calicial*); *c.*, canal of spermatheca; *d.*, oviduct; *e.*, developing egg; *f.*, wall of basal ovarian follicle; *gr.*, germarium; *h.*, head of spermatheca; *k.*, egg-calyx; *m.*, median ligament; *n.*, nucleus or germ-disc; *ov.*, ovarioles; *p.*, basal follicle or pedicel; *s.*, ovarian suspensorium; *so.*, spermathecal opening; *t.*, basal portion of terminal filament of ovariole; *v.*, common oviduct; *vo.*, vaginal opening; *vt.*, vitellarium.

ovaries are whitish, translucent bodies which measure about 7 mm. in length and 3 mm. in width and lie dorsal to the alimentary canal in the 4th to 6th abdominal segments. Each ovary is composed of a large and varying number of ovarioles (*ov.*). Each ovariole (Text-fig. 1*b*) consists of a chain of developing egg-cells, the oldest being at the base; towards the apex the ovariole passes into the terminal filament (*t.*). The ovarioles are disposed obliquely. The terminal filaments of the various ovarioles unite to form a median ligament (*m.*) which leads into the ovarian suspensorium (*s.*). The latter, in its turn, is attached to the dorsal body-wall of the mesonotum and holds the ovary in position. The ovarioles in each ovary lie close together in an obliquely longitudinal row of about 15-25 in a row, and roughly 2 or 3 deep. Each ovariole abuts on a muscular tube, the egg-calyx (*k.*), of its side which leads into the short (about 5 mm. long) oviduct (*d.*). The latter passes beneath the apodeme of the subgenital plate (8th sternum) and then bends inward to unite, below the alimentary canal, with its fellow of the opposite side to form the common oviduct or vagina (*v.*). The vagina opens into the "genital cavity" (*i.e.*, the exterior) near the posterior margin of the subgenital plate. In the same cavity, but more dorsally, lies the *independent* opening (*so.*) of the spermatheca[1]. Anteriorly, each egg-calyx leads into a single, blind, tubular and convoluted accessory gland or *boyau calicial* (*b.*); abnormally, the *boyau calicial* may possess an additional pouch (Roonwal, 1935). With maturity, the ovaries increase in size and also assume a yellow colour due to yolk in the ripening eggs. In a female about to oviposit the ovaries occupy the whole of the abdomen and also extend into the thorax; they then measure about 26 mm. long and 11 mm. wide.

THE NUMBER OF OVARIOLES IN ADULTS AND HOPPERS.

A total of 85 adult females from swarms was examined (Table 6), but later some of the readings were accidentally lost and only 49 were available for some purposes (Tables 1-4).

Table 1.

Number of ovarioles in right and left ovaries in 49 females of *Schistocerca gregaria* (phase *gregaria*, from swarms).

Serial No.	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13*	*14*	*15*	*16*	*17*	*18*
Rt. ovary	43	45	46	46	47	48	48	49	49	49	49	50	51	52	52	53	53	53
Lt. ovary	49	54	54	54	48	55	52	54	52	58	54	53	54	53	76	40	63	53

[1]Qadri's (1940, p. 156) statement that the spermatheca opens on the common oviduct is incorrect both for *Locusta migratoria* (*vide* also Boldyrev, 1929; and several others) and *Schistocerca gregaria* (Karandikar, 1942; and the present account.) In fact in all the Acrididae so far studied the spermathecal opening is independent of the vaginal opening.

Table 1—continued.

Serial No.	*19*	*20*	*21*	*22*	*23*	*24*	*25*	*26*	*27*	*28*	*29*	*30*	*31*	*32*	*33*	*34*	*35*	*36*
Rt. ovary	53	54	54	54	55	55	56	56	57	57	57	57	57	58	58	58	58	58
Lt. ovary	53	53	47	53	63	53	81	50	56	52	54	51	51	72	55	58	48	59

Table 1—concluded.

Serial No.	*37*	*38*	*39*	*40*	*41*	*42*	*43*	*44*	*45*	*46*	*47*	*48*	*49*
Rt. ovary	59	64	64	68	68	70	70	72	73	73	73	74	83
Lt. ovary	51	57	45	68	53	66	73	73	68	72	69	69	53

Table 2.

Frequency distribution, etc. of the total number of ovarioles in the right and left ovaries of 49 individuals. [From Table 1.] *n*, number of ovarioles ; *f*, frequency. (In the numerals within the range of *n* which are omitted, *f*=0.)

(*a*) Right ovary. *Range* 43-83 ; *mean* 57·3.

n	43	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	64	68	70	72	73	74	83
f	1	1	2	1	2	4	1	1	2	4	3	2	2	5	5	1	2	2	2	1	3	1	1

(*b*) Left ovary. *Range* 40-81 ; *mean* 57·2.

n	40	45	47	48	49	50	51	52	53	54	55	56	57	58	59	63	66	68	69	72	73	76	81
f	1	1	1	2	1	1	3	3	8	8	2	1	1	2	1	2	1	2	2	2	2	1	1

Table 3.

Frequency distribution, etc. of the difference in the number of ovarioles in the right and left ovaries in each of the 49 individuals. [From Table 1.] *d*, difference; *f*, frequency. (In the numerals within the range of *d* which are omitted, $f=0$.)

Range 0-30; *mean* 6·5.

d	0	1	2	3	4	5	6	7	8	9	10	13	14	15	19	24	25	30
f	4	8	1	6	3	5	4	3	4	2	2	1	1	1	1	1	1	1

The total number of ovarioles (in the right and left ovaries together) varied in 49 individuals from 92-145, mean 114·5 (Table 4). The number of ovarioles in the right and left ovaries in different individuals (Table 2*a*, *b*) varied from 43-83 (mean 57·3) in the right ovary, and 40-81 (mean 57·2) in the left; there is, thus, no appreciable difference in the mean number of ovarioles in the right and left ovaries of different individuals. In the same individual, however, the number of ovarioles in the right and left ovaries is usually asymmetrical (Table 3), the difference ranging from 0-30 (mean 6·5). As will be seen from Table 4, there appears to be no apparent relation between the difference in the number of ovarioles in the right and left ovaries and the total number of ovarioles in the two ovaries.

Regarding the mode of origin of this asymmetry, the following, I believe, provides a fairly satisfactory answer. Examination of a few hoppers of second to fifth stages[2] showed (Table 5) two significant features: (i) That the number of ovarioles in the hoppers is already large (2nd stage 118, 126; 3rd stage 116, 124; 4th stage 108, 116; 5th stage 116, 136). The number even in the second stage hopper most probably represents the full quota for the adult stage of that individual, since the number in the hopper stages is not appreciably smaller than that in the adult (*cf.* Table 4). It may be added that the ovarioles are already differentiated in the freshly-hatched first stage hopper, but, owing to their extreme compactness, their number could not be accurately counted; I am certain, however, that this number is large. (ii) That in all the eight cases, the number of ovarioles in the right and left ovaries is symmetrical.

[2] In the *grejaria* phase the Desert Locust has 5 hopper stages, exclusive of the vermiform larva. The 5th stage hopper moults into the adult.

Table 4.

Frequency distribution, etc. of the total number of ovarioles in the two ovaries in each of the 49 individuals. [From Table 1.] *t*, total number ; *f*, frequency ; *d*, difference between right and left ovaries. (In the numerals within the range of *t* which are omitted, *f*=0.)

Range 92-145 ; *mean* 114·5.

t	92	93	95	99	100	101	103	105	106	107	108	109	110	111	113	116	117	118	121	128	130	136	137	141	142	143	145
f	1	1	1	1	3	2	4	2	4	3	3	2	1	1	2	2	1	1	2	1	1	3	1	1	1	2	2
d	6	13	1	9	4-8	3-7	3-7	1-3	0-10	1-9	2-6	5-19	8	3	1-3	0-10	1	8	7-15	24	14	0-30	25	5	4	3-5	

Table 5.

Number of ovarioles in the right and left ovaries in 8 hoppers of 2nd to 5th stages. *Rt.*, right ovary; *Lt.*, left ovary.

Stage	2nd		3rd		4th		5th	
Ovary	*Rt.*	*Lt.*	*Rt.*	*Lt.*	*Rt.*	*Lt.*	*Rt.*	*Lt.*
Number of ovarioles	63	63	58	58	54	54	68	68
	59	59	62	62	58	58	58	58

Again, a comparison of freshly eclosed or very young females with older females (nearing maturity or already mature) shows that in the 85 females which were examined (Table 6) the proportion of symmetrical or nearly symmetrical ovaries was much higher in young (42%) than in older females (29%). The criterion of symmetry adopted was that the difference in the number of ovarioles in the right and left ovaries in a female should not exceed 2.

Table 6.

Number and percentage of hoppers and adult females with symmetrical or nearly symmetrical ovaries.

Stage	Total number examined	Cases with symmetrical or nearly symmetrical ovaries	
		Number	%
Hoppers (2nd-5th stages)	8	8	100%
Freshly eclosed or very young females	19	8	42%
Females nearing maturity or already mature	66	19	29%

Though the number of specimens examined was rather small, the presence of symmetry in the hoppers and the greater frequency of symmetry in very young females as compared to mature ones, strongly suggest that the asymmetry is acquired not earlier than either the late hopper stages (late 5th) or some time after eclosion. The asymmetry probably arises by the unequal resorption in the right and left ovaries of the already differentiated ovarioles caused by competition for space and nutriment in a rapidly developing ovary crowded with ovarioles. This view finds support from the following observations.

In the ovary of a freshly hatched hopper all the ovarioles are of approximately the same size. Already in the fourth stage it is noticed that some ovarioles are markedly smaller than the others. In a mature female about to oviposit for the first time, though the majority of the ovarioles are large and each contains a ripe yellow egg in the basal follicle, there are some which are extremely underdeveloped and do not contain ripe eggs. This feature, incidentally, explains why the number of eggs laid is not equal to the number of ovarioles present in an ovary. Regarding the origin of the difference in the development of the various ovarioles which compose an ovary, there are two possibilities: (i) That the first differentiation of the ovarioles in an ovary does not occur at the same or nearly the same time. This is unlikely since the full quota of ovarioles is evidently differentiated even as early as the 2nd hopper stage (probably earlier), as is suggested by their large number and almost equal size in the early hopper stages. (ii) That in an ovary some ovarioles, though at first they start developing together with the others, lag behind in later development due to competition for space and nutrition. Owing to the causes already mentioned, some ovarioles are completely resorbed but in varying numbers in the right and left ovaries, thus leading to asymmetry.

SUMMARY.

1. The ovary of the Desert Locust is briefly described.

2. The number of ovarioles was examined in several adult females of phase *gregaria* (from swarms) and a few phase *gregaria* hoppers of second to fifth stages, and their natural variation analysed.

3. The total number of ovarioles in the two ovaries (right and left) varied in 49 females from 92-145, mean 114·5.

4. There was no significant difference in the mean number of ovarioles in the right and left ovaries in different individuals. The figures for 49 females were: right ovary 43-83, mean 57·3; left ovary 40-81, mean 57·2.

5. In the same female, however, the number of ovarioles in the right and left ovaries usually differs. The difference in 49 females was 0-30, mean 6·5. This asymmetry is absent in hoppers. It is evidently acquired in the late fifth stage hopper or in the young adult, and is accentuated with maturity in the adults.

6. The ovarioles are already differentiated in the freshly hatched hopper. Even in the 2nd stage hopper their number is large and probably represents the full quota for that individual; no further increase probably occurs.

7 At first (*i.e.*, in a freshly hatched first stage hopper) all the ovarioles in an ovary are subequal in size. Already in the 4th stage hopper, however, some of the ovarioles are markedly smaller than the others. The unequal development, probably caused by competition for space and nutrition, is accentuated as the ovary matures and, ultimately, a varying number of ovarioles is completely resorbed, thus leading to reduction and asymmetry in the right and left ovaries. The unequal development also explains why the number of eggs laid is smaller than the number of ovarioles.

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