STUDIES IN INTRASPECIFIC VARIATION.

IV—THE ROLE OF SOME VARIATIONS, *E.G.*, EYE-STRIPES, ETC., AS "POPULATION INDICATORS" IN THE DESERT LOCUST, AND THEIR PRACTICAL IMPORTANCE.[1]

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CONTENTS.

INTRODUCTION.

A certain irregular periodicity in population fluctuation in certain species of locusts is well-known. In the Desert Locust, *Schistocerca gregaria* (Forskål), there is evident, *on the average*, a rough 11-year periodicity in the plague years, though the individual plague periods may last from 2-10 years and may be separated by non-plague periods lasting from 1-8 years (Uvarov, 1928; Rao, 1941). In the plague years swarming occurs in enormous numbers and the population may run into several-thousands (usually considerably over 10,000) per square mile. In the non-plague or "solitary" years the population does not go far beyond about 1,000 per square mile, and is usually less, as is clear from the study of several workers (including my own field observations in the western Indian Desert and Baluchistan) in almost the entire belt of the dry, hot desert areas from N. Africa to India. It further strikes the observer that even this low population, when studied in a restricted area, is in a continual state of fluctuation, varying from month to month.

The Phase Theory (Uvarov, 1921-1928) marked a great advance in the understanding of locust fluctuations. Attempts at what may be called "generalizations" or "large-scale explanations" of periodicity, however, continue to be made. Two recent instances concerning the Desert Locust may be cited. Bodenheimer (1937) has attempted to explain periodicity on the basis of a difference in the number of annual generations between the migration and the non-migration periods, potential increase, environmental resistance, and so on. Bodenheimer's account contains some interesting ideas. Most of his conclusions, however, are poorly supported by facts, or are based on incorrect assumptions. His scheme of the building up of outbreaks runs in the following sequence: Population ebb; preparatory years (2-6 generations); prodromal years (1-3 generations); eruption (2-10 generations); crisis (1-2 generations); and population ebb (a few to many generations).

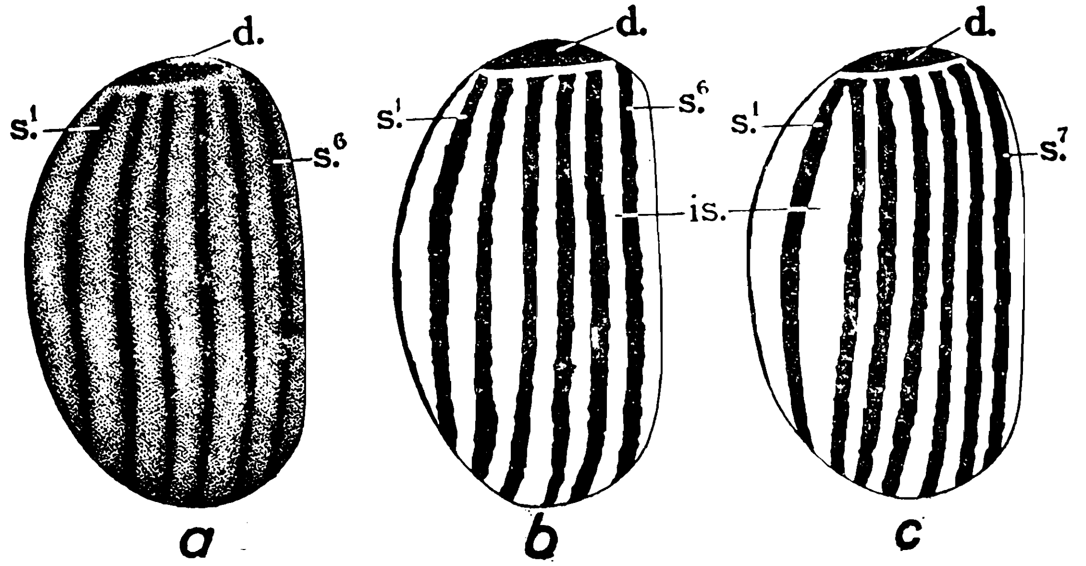
[1] Previous parts as follows:—I, *Rec. Indian Mus.* XLIV, pp. 369-374 (1946); II, *Indian J. Ent.* VII, pp. 77-84 (1946); III, *Rec. Indian Mus.* XLV, pp. 149-165 (1947).

The precise meanings of the terms "preparatory", "prodromal", "eruption" and "crisis" are left unexplained. But even if we give an approximate meaning to them, field experience shows such differentiation to be devoid of any significance. All that can be distinguished are the plague years (usually showing a peak) with high population, and the non-plague years with a low but fluctuating population. The number of generations assigned by Bodenheimer to each period has no basis in fact. Regarding the inaccuracy of the other assumptions on which Bodenheimer proceeds, three examples will suffice. Firstly, he writes that all the species of locusts, such as those of the genera *Schistocerca, Locusta, Calliptamus* and *Dociostaurus*, which migrate extensively are able to develop more than one annual generation in their gregarious phase, while the solitary phase has only one generation. So far as *Schistocerca gregaria* is concerned, we know that *both* the *solitaria* and *gregaria* phases have 2-3 annual generations. Secondly, Bodenheimer considers the "Sudano-Deccanian" region (extending from Sudan in N. Africa to the Deccan in India) as the permanent home of the Desert Locust. We know difinitely that the Deccan is not the permanent home—the locusts reaching the Deccan only in very exceptional swarming years and never breeding there (Rao, 1945). Thirdly, his statement that the mortality of adults during the so-called imaginal diapause is certainly very great cannot be substantiated. There is no diapause in any stage in the Desert Locust; only, during the cold months, as compared to the summer months, development is very much slowed down and the life-duration prolonged. Nor is there any evidence in support of his assertion that the mortality is greater in the winter than in summer months.

The second instance of a "large-scale explanation" is the interesting attempt of Rao (1938) to correlate Desert Locust periodicity with the sun-spot cycles in India. Rao concluded that a negative correlation subsists between locust cycles and sun-spot numbers. An examination of his numerical data and graph, however, shows that, as in so many previous attempts on locusts and other animals, the supposed correlation is so approximate and breaks down at so many points that the few points where the correlation does occur would seem to be fortuitous rather than real.

These two instances demonstrate the great limitations of such large-scale explanations. The more fruitful, though tedious, procedure then is to make a close study of population dynamics, character by character, from samples obtained periodically in the field. This procedure resolves itself into two methods of approach: (i) *Direct counting*: This involves the periodic counting of actual numbers in a given area. For the Desert Locust, this has been done during approximately the last 15 years in India and Africa by several workers. To start with, it is the only sure method. (ii) *Indirect assessment*: In locusts the morphological and other characters change with population density. So that, if the changes in these characters can first satisfactorily be correlated with actual population figures obtained by the first procedure, they can then be employed as "*population indicators*", thus obviating the necessity of direct counting. The value of the second procedure depends entirely on the ease and accuracy of determination of the population indicators. In the present account the value of some of the indicators in the study of Desert Locust populations is discussed.

Biometrial ratios, especially E/F (elytron-length/hind-femur-length), have for many years been the stand-by for population studies of locusts, and the accumulated evidence from several species of locusts tended to show that E/F is quite a sensitive guide to phase. Recently, however, Kennedy (1939, pp. 400-405), from a study of Desert Locust population in an outbreak centre on the Sudanese coast of the Red Sea, found that the E/F ratio alone is not a safe guide. He concluded as follows (p. 404): " Thus it seems that the E/F ratio and other biometric features are unsafe criteria of phase unless account be taken of the stage of given individuals in the whole cycle of outbreak and non-outbreak years, covering many generations. A population which appears a fully gregarious swarm may be biometrically *solitary* if it comes among the early swarms of an outbreak and *vice versâ*, apparently solitary locusts may be biometrically ' gregarious ' if they appear at the end of an outbreak period." It, therefore, becomes necessary to seek also the aid of other characters besides the biometrical ratios for the study of phase and population dynamics.

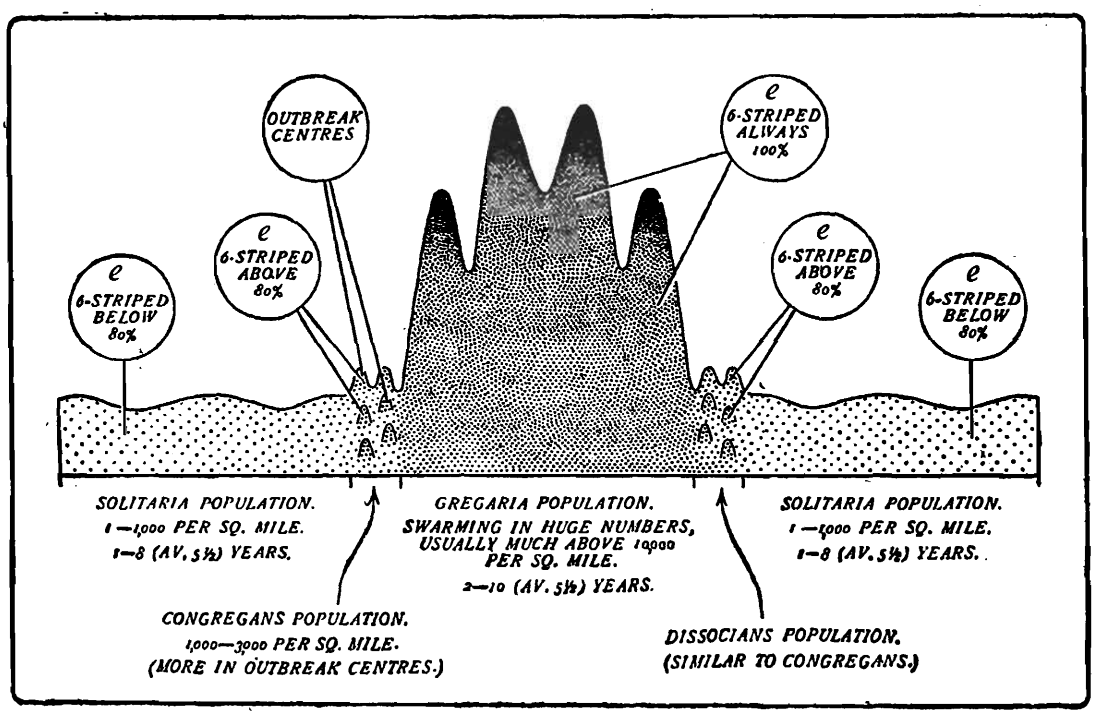


TEXT-FIG. 1.—Compound eyes of the Desert Locust, *Schistocerca gregaria* (Forskål). × about 10. Anterior margin of eye is on the right. (*a*), in phase *gregaria* (6-striped). (*b*) and (*c*), phase *solitaria*, 6- and 7-striped respectively. [(*b*) and (*c*) after Roonwal, 1936.]

d., dorsal pigment spot of eye; *is.*, interstripe; s^1., first or most posterior stripe; s^6., s^7., sixth and seventh stripes respectively.

Some years ago, I reported (Roonwal, 1936) on another character, *viz.*, the presence of a variable number of eye-stripes (usually 6 and 7) (Text-fig. 1*b*, *c*) in a *solitaria* population of the Desert Locust, which has proved to be of considerable importance in population study, *vide* Rao (1937, p. 41). Further work followed rapidly and the development of the eye-stripes was studied first by Roonwal (1937, 1947) and later by others (Volkonsky, 1938; Mukerji and Batra, 1938). It was found that a vertical stripe first develops in the first stage hopper, and subsequently, one stripe (rarely two or none) is usually added at each moult. In the course of my later work, it was found that the eye-pigment in the Desert Locust first appears in the embryo shortly before blastokinesis as a faint orange-red pigment at the posterior border of the compound eyes, and soon turns brownish.[2] The same thing had been noticed earlier (Roonwal, 1936*a*, p. 415) in the African Migratory Locust, *Locusta migratoria migratorioides* (R. & F.), in which, however, the eyes are unstriped. It was also shown (Rao, 1937 ; Rao & Gupta, 1939 ; Roonwal, 1941) that *gregaria* individuals of the Desert Locust from swarms always have 6-striped eyes[3] (Text-fig. 1*a*).

From a comparative study of eye-stripes in *solitaria* and *gregaria* populations over a number of years, three tentative hypotheses were advanced (Roonwal, 1945) for the determination of population fluctuation. The First Hypothesis is as follows : " If in a sufficiently large sample of a *solitaria* population the proportion of the 6-eye-striped individuals (in relation to 7-striped ones) rises above about 80 per cent (maximum figure ; average 70·4 per cent) and tends towards 100 per cent, that population is rapidly on its way towards swarming. Conversely, if in a *gregaria* population the proportion of 6-striped individuals falls below 100 per cent and tends towards 80 per cent, that population is on its way towards the acquisition of *solitaria* or non-swarming characters" (Text-fig. 2).



TEXT-FIG. 2.—Diagrammatic representation of the periodical population fluctuation in the Desert Locust, and its relation to the eye-stripe figure *e*.

The number of peaks and valleys in the figure has no exact quantitative significance. The papillae in the region of the *congregans* population (left) represent "outbreak centres", while similar papillae in the *dissocians* population (right) represent isolated pockets of high population before the dispersal leading to low populations (characteristic of the *solitaria* periods) occurs.

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[2] For a study of early embryos of the Desert Locust, *vide* Jhingran, 1947.

[3] Formerly it was believed that in *gregaria* individuals the eyes are unstriped owing to the interstripe region being invaded by brown pigment. Actually, the stripes can be seen in several specimens, though they are usually less sharply contrasted than in *solitaria* individuals—*vide* Roonwal, 1947.

In the present account a more detailed analysis has been attemped of the available data in terms of the First Hypothesis. The analysis supports the essential points of that hypothesis, and further shows that the eye-stripes provide an excellent "indicator" for the study of population dynamics. Two new theoretical conceptions—one that of the E/F shift figure g, and the other of the eye-stripe figure e —are put forward; these are likely to be of considerable help in the study of populations. Finally, the practical importance of the eye-stripe "population indicator" in anti-locust work is explained.

I am greatly obliged to Dr. B. N. Chopra for helpful criticism of this paper, and to Dr. B. S. Chauhan for assistance in correcting the proofs.

TWO NEW CONCEPTIONS: E/F SHIFT FIGURE g AND EYE-STRIPE FIGURE e.

E/F shift figure g.

The ratio E/F increases with increasing population density, being higher in phase *gregaria* and lower in *solitaria.* In this regard a population is customarily (Rao, 1936-1942; Roonwal, 1947*b*; and others) grouped into three categories, namely, *solitaria* (S), *transiens* (T) and *gregaria* (G), with the following limits:—

S: E/F 2·05 and below to about 1·85.
T: E/F 2·06-2·15.
G: E/F 2·16 and above to about 2·43.

The number of individuals in each category gives an idea of the character of the population. Rao (1942) has used the following percentage form for expressing the population character in terms of the three classes, S, T and G, based on E/F ratios, and also in terms of the proportion of 6- and 7- eye-striped forms :—S:T:G : : (6) : (7). By the side of each item is given the number or percentage of individuals in each category in the population sample, *e.g.*, 62S : 29T : 9G : : 67(6) : 33(7). As, however, *transiens* is a category which it is impossible to distinguish satisfactorily, in so far as coloration and general facies are concerned (*vide* also Part III, Roonwal, 1947*b*), it seems desirable to divide a population sample into two categories only, namely, *solitaria* (S_1) and *gregaria* (G_1), with the following limits:—

S_1: E/F 2·10 and below.
G_1: E/F 2·11 and above.

Where a population is expressed in terms of S, T and G, it can be converted into S_1 and G_1 by dividing T equally between S and G, thus:

$$S_1 = S + \frac{T}{2}\text{; and } G_1 = G + \frac{T}{2}$$

The numbers in the categories S_1 and G_1 are then converted into percentages s and g respectively, of the total number of individuals. These percentages indicate how far the population sample is removed from either the *solitaria* or the *gregaria* end. In other words, they express the *shift* (towards *gregaria* or *solitaria*) of a population, so that they may, for brevity, be called *E/F shift figures* s and g. Since s and g are complementary to each other ($s = 100 - g$), it is necessary to mention only

TABLE

Periodical analysis of Desert Locust populations with regard to field observations) in solitaria *periods* (*except the July 1935*

Abbreviations : e, eye-stripe figure for 6-striped

g, E/F shift figure towards *gregaria* phase ;

S, *solitaria ;* T, *transiens ;* and

Sol., *solitaria ;* and Gr., *gregaria* population, as judged by

Dominating phase ; and population per sq. mile	Serial number of sample	Region and period	Number of individuals					
			Total	Eye-stripes		E/F		
				6	7	S	T	G
		INDIA. *Mekran Coast.*						
Sol. (100)	1	Jan.—Mar., 1935	..	..	..	..	..	..
Sol. (460)	2	Apr.—May, 1935	..	..	..	..	..	..
Gr. (13,000)	3	July 1935 (incursion)	..	..	..	..	..	..
		Sind-Rajputana.						
Gr. (40,000)	4	July 1935 (incursion)	..	..	..	..	..	..
Sol. (Low)†	5	Oct.—Nov., 1935 (new brood).	..	..	..	..	..	..
		Lasbela.						
Sol. (720)	6	Dec. 1935	..	..	..	..	..	..
		INDIA.						
		S. Mekran.						
Sol. (120)	7	Mar. 1936	58	21	37	33	22	3
Sol. (30)	8	Apr. 1936	14	4	10	7	7	0
Sol. (550)	9	May 1936	61	43	18	28	30	3
Sol. (660)	10	June 1936	96	59	37	51	39	6
Sol. (480)	11	July 1936	27	18	9	11	16	0
Sol. (190)	12	Aug.-Sept., 1936	30	22	8	13	15	2
Gr. (Swarms)	13	*Indo-Iranian region* . (1889-91 ; and 1930-31)	41	41	0	1	4	36
		N. AFRICA.						
		Central Sahara.						
		(Periods not stated.)						
Sol. (Probably low).	14	In Salah (Tidikelt) ..	70	24	46	..	..	..
Sol. (Probably low).	15	Reggan (Touat). ..	82	28	54	..	..	..

† The new brood population figures for October-November 1935 in the Sind-Rajputana desert area
outside, as indicated by sudden increases ; and (ii) by its rapidly declining density from October onward.
mile) in October, but rapidly declined in November to barely a few hundred per square mile; in some
in the succeeding one or two months. The population in question must, therefore, be considered

1.

eye-stripes and phase (as judged from E/F, together with actual incursion of gregaria *forms in India).*

individuals; e_1, same for 7-striped individuals.

s, same towards *solitaria* phase.

G, *gregaria* range of E/F.

actual field observations as well as on other criteria.

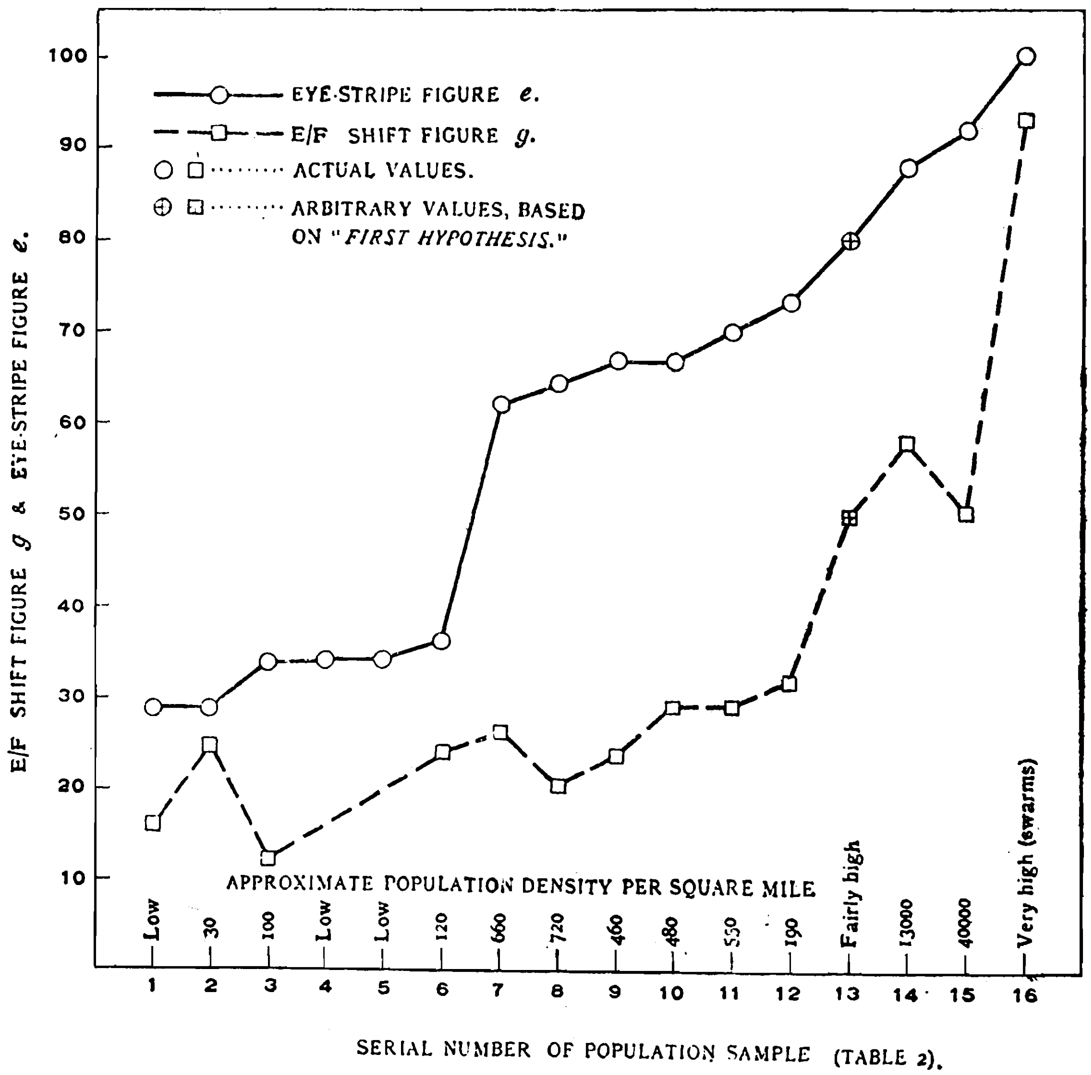
% of individuals					E/F shift figure		Source
Eye-stripes		E/F					
6 (*e*)	7 (e_1)	S	T	G	*s*	*g*	
34	66	76	28	1	87·5	12·5	
67	33	62	29	9	76·5	23·5	
88	12	24	35	41	41·5	58·5	
92	8	28	43	29	49·5	50·5	Rao, 1936*a*, 1937, 1942. (E/F shift figures calculated by me.)
29	71	69	30	1	84·0	16·0	
64	36	59	41	0	79·5	20·5	
36	64	57	38	5	76	24	
29	71	50	50	0	75	25	
70	30	46	49	5	70·5	29·5	Original.
62	38	53	41	6	73·5	26·5	
67	33	41	59	0	70·5	29·5	
73	27	43	50	7	68	32	
100	0	2	10	88	7	93	
34	66	Phase *solitaria*.			..	..	Volkonsky, 1938.
34	66	Phase *solitaria*.			..	..	

are complicated by two factors: (i) By probable immigration from
Thus, the population was rather high (several thousands per square
places hardly any locust was found in the last week of November and
essentially of a low density, a conclusion borne out by the low *g* and e_1

one of them for a population sample—the adoption of *g* (shift towards *gregaria*) is proposed. Theoretically, in a wholly *gregaria* population (swarms), $g=100$ and $s=0$; while in a wholly *solitaria* population (middle of non-swarming period), $g=0$, and $s=100$. In actual practice, these ideal conditions are not met with. Thus, in a small sample of Desert Locust population from actual swarms in the Indo-Iranian region, the figures were : *g* 93, *s* 7. Similarly, in a typical *solitaria* period, as for example in Southern Baluchistan in January-March 1935 and during 1936, the figures for the population sample with the lowest *g* were : *g* 12·5, *s* 87·5.

The already mentioned criticism made by Kennedy (1939) is here relevant. But it is of great theoretical interest to know that even in the " peak " or middle years of each swarming or non-swarming period, a certain small percentage of individuals belong to the phase-group which is characteristic of the other period.

It may be tentatively assumed that the dividing line between *solitaria* and *gregaria* populations is at $g=50$. Actually, perhaps, this figure may prove to be a little too high, but it may be adopted until more data are available.



TEXT-FIG. 3.—Graph showing the correlation between the E/F shift figure *g* and the eye-stripe figure *e* in several population samples (Table 2) of the Desert Locust.

Eye-stripe figure e.

Since only 6- and 7-eye-striped individuals concern us in any sample of Desert Locust population (the 5- and 8-striped individuals occurring far too rarely to be of much practical importance), it is convenient to reduce the number in each category to percentages. The term *eye-stripe figure* may be used for these percentages—abbreviated to e for 6-striped and e_1 for 7-striped forms. Since in a population sample, e and e_1 are complementary ($e=100-e_1$), it is necessary to mention only one of them—the adoption of e is proposed. In a typical *gregaria* population (swarms), e always equals 100, and e_1 equals 0. In typical *solitaria* populations, as for example those mentioned above under g, the minimum value reached by e is about 29.

Thus, if a population sample is expressed as: g 23·5, e 67, we will know that in this sample 23·5 per cent. individuals have *gregaria* E/F ratios, and the remainder *solitaria*; further, 67 per cent. individuals have 6 eye-stripes, and the remainder 7 stripes. The use of the simplified conceptions g and e for the Desert Locust will become evident from what follows. They are also likely to prove helpful in the study of those of the other species which, like the Desert Locust, have striped eyes.

ROLE OF " POPULATION INDICATORS " : CORRELATION BETWEEN e AND g.

In 1935 in Western India the June *solitaria* population of about 500 adults per sq. mile suddenly rose, in middle July and August, to about 20,000, and in some places even up to 40,000 (Rao, 1936). This was due to an incursion from the west (Iran or Arabia) of *gregaria*-like individuals and it looked as if a new swarming period was on. The incursion, however, fizzled out, and by December the population was again about 300 per sq. mile. In this change, the E/F was found to be a sensitive guide to the population-character (density), the immigrating individuals in July having mostly high or *gregaria* ratios, while the *solitaria* population preceding and following (next generation) the immigration having low or *solitaria* ratios (Rao, 1936). As will be shown below, in this change in population character, the eye-stripe figure e is correlated with the E/F or shift figure g, and is, like the latter, an excellent indicator of the population dynamics.

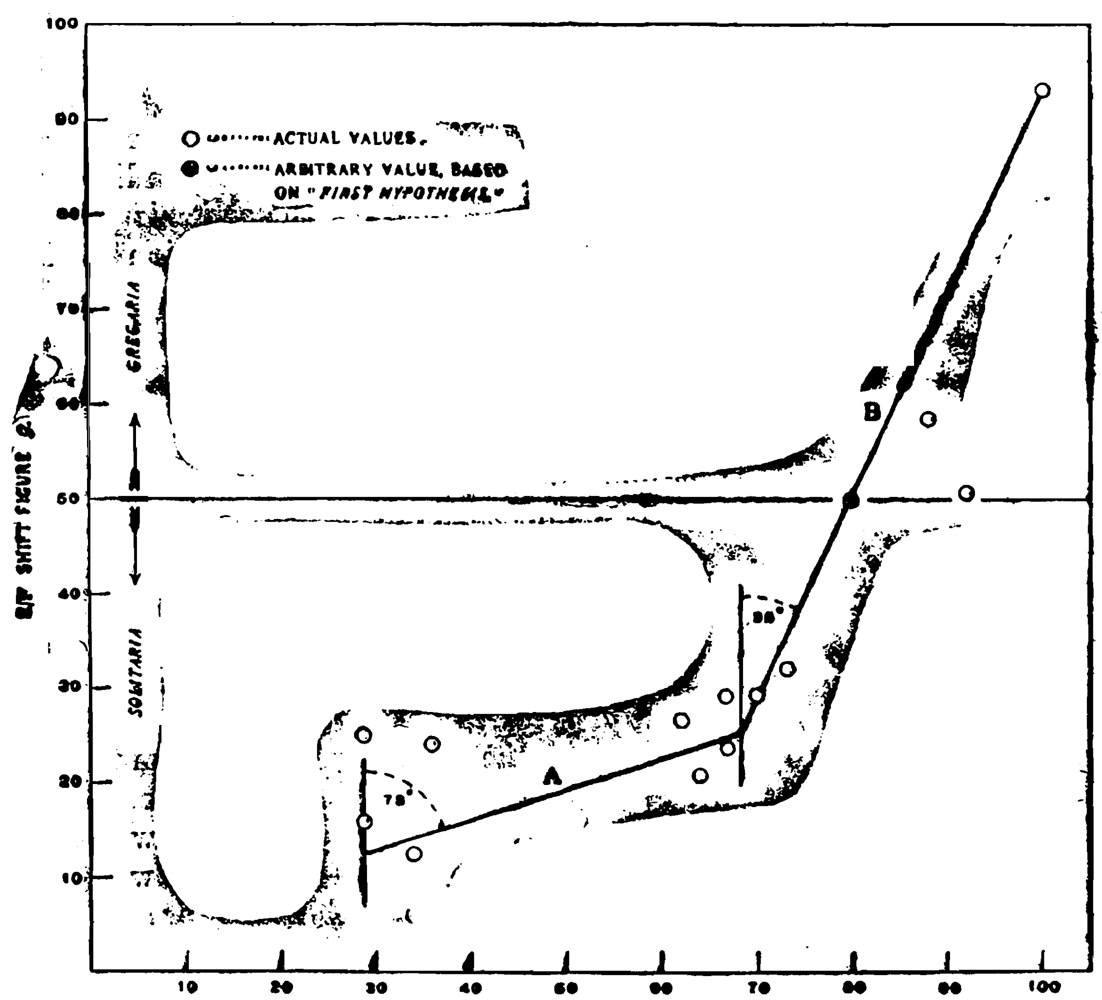
In Table 1 are given the published E/F shift-figure g and eye-stripe figure e from the data of Volkonsky (1938) and Rao (1942), together with my own figures for *solitaria* populations in S. Mekran (Baluchistan) in 1936 and of a *gregaria* population from the Indo-Iranian swarms of older cycles. In the case of Rao's data, S, T and G were given, from these I have calculated the E/F shift figures s and g by the method already described. With the exception of Sample Nos. 3 and 4 which refer to the July 1935 incursion of *gregaria* individuals (*vide supra*), and No. 13 which refers to true swarms, all the other samples are from typical *solitaria* populations, known to be so from actual field experience and belonging mostly to the middle year (1936) of the last non-swarming period which lasted in India from 1932 to 1939—the new swarming period started in 1940. In Nos. 14 and 15, no E/F ratios are given, but Volkonsky states that the populations were *solitaria*, and we may assume that g was below 50.

Regarding g, three points will be noticed : (*i*) In *solitaria* populations g varies from 12·5-32, *i.e.*, its value lies definitely below 50 ; (*ii*) in the July 1935 incursion (Sample Nos. 3 and 4) g definitely rose above 50 ; it varied between 50·5-58·5 ; (*iii*) in swarms (Sample No. 13) g was 93, *i.e.*, close to 100. Regarding e also, we notice three points : (*a*) In *solitaria* populations it varies from 29-73 ; (*b*) in the July 1935 incursion it rose to 88-92 ; (*c*) in swarms it is always 100.

In Table 2 the data of Table 1 are arranged in the order of increasing e, along with the corresponding g, in order to show the correlation between e and g. From Table 2 and Text-fig. 3 it will be seen that g generally increases with e. Although this does not happen in every case, the general tendency is perfectly clear, and may be summarized thus :

	e	g
1. *solitaria* or very low population	29-73	12·5-32
2. July 1935 incursion (population about 10,000 to 40,000 per sq. mile)	88—92	50·5-58·5
3. *gregaria* or very high populations (swarms)	100	About 93.

When e is plotted as a function of g (Text-fig. 4), it is possible to discern two separate trends of correlation (lines A and B) between e and g. In *solitaria* or low populations (lower one-third of the figure), g increases slowly in respect of e, the line A sustaining an angle of roughly 73° with the ordinate. In the upper two-thirds of the figure, *i.e.*, as we move toward the *gregaria* belt of high population, g increases very steeply in respect of e, the line B sustaining an angle of only about 26° with the ordinate.



TEXT-FIG. 4.—Graph obtained when the eye-stripe figure e is plotted as a function of the E/F shift figure g in the Desert Locust.

Table 2.

Values of e *and the corresponding* g *(from Table 1) arranged in the order of increasing* e.

Serial number.	1	2	3	4	5	6	7	8	9	10	11	12	13*	14	15	16
e	29	29	34	34	34	36	62	64	67	67	70	73	(80)	88	92	100
g	16	25	12·5	..	..	24	26·5	20·5	23·5	29·5	29·5	32	(50)	58·5	50·5	93
Approximate population density per sq. mile	Low	30	100	Low	Low	120	660	720	460	480	550	190	Fairly high.	13,000	40,000	Very high. (Swarms.)
General character of population	*Solitaria.* Very low population.												*Gregaria* predominating. Fairly high population.			Almost entirely *gregaria.* Very high population (Swarms).

* Figures in this column are arbitrary, the *e* being based on the *First Hypothesis* (Roonwal, 1945), and *g* on considerations discussed in the text.

The results of the detailed analysis given above substantiates my *First Hypothesis* already referred to.

PRACTICAL UTILITY OF THE "POPULATION INDICATORS"

The problem of Desert Locust control is such that vast continental areas from India to N. Africa, mostly deserts, have to be kept under observation by means of periodical field surveys. A considerable proportion of field reporting has to be done by the non-scientific personnel, the scientific personnel doing mainly the supervisory work in the field and the study of all the incoming data at the Central Headquarters of a country or area. The field reports usually indicate, in addition to the information on breeding, etc., the number of locusts caught or observed in a day's survey, the distance covered and the number of individuals taking part in the survey. From these data the density of locust population is obtained by means of certain well-tried formulae (Rao, 1936, p. 1036 ; 1936*a*, p. 3 ; 1942, p. 252).

If, however, the field reports were also to contain particulars about the "population indicators" (E/F and eye-stripes), they would become considerably more useful. The determination of E/F and its shift figure g requires accurate measurements of E and F with a vernier calliper which the non-scientific field staff may not be able to do satisfactorily. On the other hand, the number of eye-stripes can be accurately counted with ease by means of a hand-lens, and the eye-stripe figure e calculated. If e goes above 80, incipient swarming is indicated and the Central Headquarters must be warned at once. It is, therefore, suggested that eye-stripe counts should become a routine procedure in Desert Locust surveys. Since the eye-stripes sometimes get distorted after death, it is desirable that their number should be recorded in the fresh specimen.

SUMMARY.

1. The role of the eye-stripes as "population indicators" in the study of the population dynamics of the Desert Locust is discussed.

2. Two new theoretical conceptions, *viz.*, that of the "E/F shift figure" g and of the "eye-stripe figure" e, are given, and their importance in the study of Desert Locust populations explained.

3. The correlation between e and g has been established by a detailed analysis of the available data from various population samples.

4. The practical utility of the eye-stripes as "population indicators" in the scouting work carried out by anti-locust organizations is explained. The need for the adoption of this "indicator" as a routine method of population study in Desert Locust surveys is stressed.

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