STUDIES IN INTRASPECIFIC VARIATION.

I. On the existence of two colour-types in the adults and hoppers of the *solitaria* phase in the Desert Locust, *Schistocerca gregaria* (Forskål). [Orthopetra, Acrididae.][1]

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Foreword.

The value of the study of intraspecific variations for the understanding of various problems of evolutionary biology needs no emphasis. Of such variations there exist numerous categories ranging from morphologically distinct geographical subspecies (many of which were formerly accorded full specific rank) to smoothly graduated clines and mere physiological races (*vide* Huxley, 1944, for summary). Recent experience has shown that every species and its lower systemetic units must be investigated intensively on its individual merits, and deductions or generalizations based on even closely allied species may often prove to be misleading and erroneous.

The Desert Locust, *Schistocerca gregaria* (Forskål), has proved to be an excellent material for the study of intraspecific variations. Apart from the ordinary allometric variations, there are, in this species, firstly, the phase variations, *viz.*, the existence of *gregaria* and *solitaria* phases (Uvarov, 1923, 1928; and others). Secondly, there are non-phasic variations of which the first instance was provided by me (Roonwal, 1936). This variation referred to the existence of two different kinds of individuals (6- and 7-eye-striped) in the *solitaria* phase. These observations were later confirmed and extended (Roonwal, 1937, 1938, 1941, 1945-1946; Rao, 1937, 1938; Rao and Gupta 1939; Volkonsky, 1938, 1938*a*; and Mukerji and Batra, 1938). As a result, we now know that in *solitaria* populations mostly 6- and 7-striped (rarely 8-striped) individuals occur, while in *gregaria* populations (swarms) only 6-striped individuals are found; occasionally, 5-striped individuals turn up in laboratory breedings.

In the present series of papers I propose to describe, in the Desert Locust, intraspecific variations particularly other than those referred to above, and also to discuss the biological significance of the variations especially concerning the eye-stripes.

Introduction.

Colour differences, in both adults and hoppers, between the two phases, *solitaria* and *gregaria*, are now well-known in the Desert Locust, *Schistocerca gregaria* (Forskål) (*vide* Uvarov, 1928). But I do not think it

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is yet known that in the *solitaria* phase we can distinguish two distinct colour-types in both adults and hoppers. In the present paper I shall describe these colour-types and discuss their probable significance.

Adults.

Künckel d'Herculais (1892) first showed that swarming adults of the Desert Locust are at first pink, but later become yellow with maturity. Johnston (1926) showed that this colour change is characteristic of *gregaria* individuals only; the *solitaria* adults are greenish when young and become greyish later, but do not change colour with maturity; this was confirmed by Ballard, Mistikawi and El Zoheiry (1932).

I have, however, noticed that after a few days of the initial greenish tinge, two colour-types can be distinguished among the *solitaria* adults. Firstly, the type comprising those individuals which are suffused with a blue-grey tinge all over the body; these constitute the majority. Secondly, the type comprising those individuals which are pale buff or fawn in overtone, without any blue-grey; these occur in very small numbers.

For brevity, the two types of *solitaria* may be known as *blue* and *fawn*. The two types are clear in specimens freshly caught in the field. With preservation, however, the colours change, and in museum specimens it is no longer possible to distinguish the two types. In 367 *solitaria* individuals form southern Baluchistan (November, 1935 to September, 1936), 335 (161♂♂, 174♀♀) or 91 per cent. were blue and 32 (19♂♂, 13♀♀) or 9 per cent. fawn.

From a careful analysis, I was unable to correlate the two types with age, sex, season, E/F ratio and the number of eye-stripes (*i.e.*, the proportion of 6- and 7- eye-striped individuals, *vide* Roonwal, 1936, 1945, 1945*a*) and phase.

Vayssiére and Lepesme (1939), from breedings in the Laboratoire central de Biologie acridienne, Paris, figure two adults of the Desert Locust (their Pl. III, figs. 3 and 5) which give a good idea of the coloration of the *blue* and *fawn* types as understood by me, though Vayssiére and Lepesme themselves interpret them quite differently. On p. 61 they describe fig. 3 (blue) as "Adulte type normal de l'élevage, 2 mois après la mue imaginale"; and fig. 5 (fawn) as "Adulte obtenu en élevage isolé". No further history is given, but the meaning of "type normal" can be partly inferred by reference to p. 44 where they state: "Les individus normaux de l'élevage son toujours du type *transiens*, parfois plus voisins du type *gregaria*, parfois plus près du type *solitaria*" And further: "Dans les conditions de notre élevage, les stades larvaire son trés voisins du type grégaire au point de vue de la pigmentation" Thus, since under the breeding conditions the hoppers were very close to the *gregaria* type in pigmentation, we may infer that these authors implied that the "type normal" adult illustrated in fig. 3 was in phase *gregaria* or at least *transiens*, in contrast to that in fig. 5 which is clearly stated to have been obtained in isolated breeding and so indicating that it was typical *solitaria*. Vayssiére and Lepesme thus imply a phase significance to these figures. From considerable field and laboratory experience regarding the Desert Locust, I can say that in general facies fig. 3, like fig. 5,

appears to be that of a *solitaria* phase individual. As regards pigmentation, there can be no doubt that fig. 3 *is not* that of a *gregaria* individual for, in that phase the immature adults are pinkish and the mature ones yellowish ; they are *never* bluish. The term *transiens* is very fluid. It is fairly useful in the study of biometrical ratios of adults and the pigmentation of hoppers. But as regards adult coloration it does not convey any clear impression, and distinction between *solitaria* and *transiens* colours is not at all possible.

HOPPERS.

Phase *solitaria* hoppers of the Desert Locust are generally known to have a bright green colour (Johnston, 1926 ; Ballard, Mistikawi and El Zoheîry, 1932 ; Faure, 1932 ; Husain and Mathur, 1936 ; and Kennedy, 1939). The majority are undoubtedly so.

Besides green hoppers, however, there occasionally turn up in laboratory breedings (briefly reported by Roonwal, 1937, p. 149 ; *vide infra*), as well as in field collections, a few fawn-coloured hoppers *without any green*. These fawn hoppers are undoubtedly *solitaria*, as judged from breeding records (isolated breeding) and from field observations. In the field, for instance, a fawn hopper may be found among a batch of 10 or 12 green ones in a desert bush. The fawn colour becomes well-marked in the older hopper stages only, especially the fourth and fifth. Exact figures were not recorded, but my impression is that the frequeney of appearance of the fawn hoppers does not exceed 10 per cent. of the total *solitaria* population, and is perhaps less. It must be emphasized that such hoppers are by no means abnormalities. Their occurrence is regular enough, and they are in no respect less healthy than green individuals. The appearance of fawn hoppers is not connected with food and such other external factors for, they occur simultaneously with green hoppers bred under identical conditions in the laboratory and also under identical conditions in the field, *e.g.*, on the same bush.

To a certain extent, according to Rao (1937, p. 24), *solitaria* hoppers tend to assume the environmental colour in the field. This evidently refers to green hoppers only, since Rao makes no mention of fawn hoppers.

Roonwal (1937) performed a number of experiments by rearing Desert Locust hoppers solitarily in small, wooden boxes, each painted on the inside in different colours, *e.g.*, lemon yellow, prussian blue, mahogany, black, dark green, signal red, white and light ochre (unpainted wood). He concluded (p. 149) as follows : " It will be seen ... that some colours were apparently simulated, whereas in others the results were indefinite. Colours which were simulated to a greater or less extent were : lemon yellow, black, dark green and white. Hoppers reared in the mahogany-coloured boxes became fawn-coloured in the fourth stage. This is not regarded as due to the mahogany box, since a hopper reared in the prussian blue box also became fawn. *Moreover, the fawn colour sporadically appears in solitary hoppers in identically coloured cages where the factor of environmental colour cannot be correlated with the colour of the hopper*" (italicized now).

These results regarding colour simulation broadly confirm those obtained in similar experiments on *Locustana pardalina* and *Locusta migratoria migratorioides* by Faure (1932) in S. Africa, although the simulated

colours are not always the same as in the Desert Locust. In Faure's experiments simulation occurred in white, black, grey, yellow and brown boxes, but not in green, pink, blue and black and orange. In this connection the experiments of Hertz and Imms (1937) on *Locusta migratoria migratorioides* are also of great interest for, they explain colour-response in terms of wave length of the light emitted by the surroundings, *i.e.*, of incident light to which the hoppers are subject.

In *gregaria* hoppers of the Desert Locust bred under identical conditions in the laboratory, Vayssiére and Lepesme (1939, p. 45.) record two extremes of colour-types with regard to background colour, *viz.*, a greenish yellow and a rose, the former type being numerically predominant; in both types the pattern is balck. They further state (p. 46) that the hoppers reared on a pale background are paler than those reared on a darker background ; no further details are given, and it is not possible to say whether this statement refers to *solitaria* or *gregaria* hoppers.

It is thus seen that, so far as the Desert Locust is concerned, though simulation to environment occurs to a certain extent, the production of fawn hoppers in the *solitaria* phase is evidently an independent phenomenon which is related neither to environment nor to phase. It seems probable that the fawn and green colour-types among hoppers of the same phase (*solitaria*) have a genetical significance. The fawn hoppers, as regards colour, remind one strongly of the fawn adults described above, and it is very probable that the two colour-types in hoppers are related to the two colour-types in adults—the fawn hoppers producing fawn adults, and the green hoppers producing blue adults. This supposition is supported by the relative frequency (of about the same degree) of occurrence of fawn hoppers and fawn adults (about 10 per cent.) on the one hand, and green hoppers and blue adults (about 90 per cent.) on the other.

Summary.

1. Two colour-types, termed *blue* and *fawn*, of *solitaria* adults occur in the Desert Locust. The blue type is predominant (91 per cent.), while the fawn type occurs less frequently (9 per cent.).

2. The occurrence of the two types of adults is not correlated with age, sex, season, E/F ratio, number of eye-stripes and phase.

3. Two colour-types also occur among *solitaria* hoppers of the Desert Locust, *viz.*, the *green* type which is common and is already well-known, and a *fawn* type which occurs rarely. This colour distinction is well-marked in the older (fourth and fifth) stages.

4. The occurrence of these two types of hoppers is not related to food and environmental factors (*e.g.*, background colour, etc.), nor to phase. It might possibly have a genetical significance.

5. It is probable, as is suggested by the relative frequency of their occurrence, that the two colour-types in the *solitaria* hoppers are related to the two colour-types in the *solitaria* adults — the green hoppers producing blue adults and the fawn hoppers producing fawn adults.

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