COLOUR VARIATION IN BRITISH ACRIDIDAE (ORTHOPT.).

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INTRODUCTION.

I propose to develop here a graphic method for the description of the colour forms of Acrididae, and to use it to record the forms I have found so far among British Acrididae, mainly in the course of an investigation of the relation of coloration to distribution which I began last summer. This work showed the need for a practical descriptive system which could cope with the complexity of the variables involved, and which would avoid theoretical implications, such as that of strictly homologous variation involved in the adoption of Rubtzov's (1935) system of named forms. In the development of the system to be described I have been greatly helped by the valuable constructive criticism of Dr. B. P. Uvarov, to whose suggestions many of the features are due.

The description of each form is by a coloration formula, composed of symbols describing in turn the general distribution of colour and the various minor details. The complexity is sometimes extreme, to the point of inconvenience, but I have tried to reduce it as far as is compatible with adequate description of the detailed features of pattern. The method of construction of the formula will permit omission of features which may be irrelevant to particular practical purposes, and so eliminate some complexity, as a complete formula is made by stringing together the symbols for each individual feature in turn. Furthermore this method, namely the summation of fragmentary features, is justified both by descriptive observation of pattern variation and by the work of Sansome and La Cour (1935), who showed that the genes concerned with the coloration of *Chorthippus parallelus* (Zett.) generally each control only a small feature of the total pattern; however, these fragmentary features are not integrated to give complete patterns by random combination, but by virtue of a high degree of epistasy and factor interaction their assortment is restricted, and a relatively small number of complete forms is produced. In general, restrictions on the random combination of minor details are not as complete as on that of major features, and the graphic designation of each feature by the colour formula is well adapted to show the minor variations within each main colour form, which would be difficult to record by any less complex means. The detailed and methodically derived nature of the formula also gives it an advantage for practical descriptive work over both systems of named forms (such as those of Vorontzovskii, 1928, and Rubtzov, *loc. cit.*) and the arbitrary symbols usually used by geneticists (*e.g.* Sansome and La Cour, *loc. cit.*).

The criterion used in deciding whether any given feature of coloration should be included in the classification has been the importance of the feature in the total colour pattern of the resting insect, irrespective of the distinction made by Rubtzov (*loc. cit.*) between features showing true homologous variation and those showing phase variation. The difference from Rubtzov's treatment of coloration is inevitable, since his was based on breeding experiments, by which he distinguished phase variation from homologous variation by comparison of stability to change of environmental conditions. The present system cannot take account of this distinction, since it is purely descriptive.

Although the system is primarily designed for the forms shown by British species, its generality has been increased by considering also in its construction a large number of colour forms among the Acrididae in the M. Burr collection of Palaearctic Orthoptera at Oxford. Thus some trivial distinctions which would have resulted from considering only the limited British fauna have been avoided, and it has also been possible to interpret the main trends of variation in terms of the operation of three tendencies to disruptive pattern among Acrididae in general. This interpretation is necessarily hypothetical, but it has the advantage of presenting problems for experimental investigation, and provides a consistent point of view for the application of the criterion of significance of each feature for the total colour pattern, even though the application may seem somewhat biassed thereby.

The three main tendencies to differentiation of disruptive pattern from the relatively simple and even distribution of colour found in some mesophilous species, *e.g.* in a large proportion of individuals of *Chorthippus parallelus* (Zett.) or *C. albomarginatus* (de Geer), will first be briefly described, before the detailed exposition of the system. I would emphasise that the main function of these conclusions is to provide a framework for interpretation of the variation of the present material; the limited number of species and short series available preclude any pretensions to their being anything more than working hypotheses.

The first tendency is comparatively insignificant, comprising longitudinal pale and dark stripes, usually on a green background; it was not found in many species in the Burr collection, but was shown strikingly by *Mecostethus grossus* (L.) and *Parapleurus alliaceus* (Germ.).

The second is shown by the brown forms of many, perhaps most, of the species of Acridinae examined; it involves longitudinal pattern markings of two types—one with the disruptive lines strictly longitudinal and the other with them slightly oblique (backward and upward on the side; backward and towards the midline on the dorsum).

Finally there is a tendency among the brown forms of the most xerophilous of the Acridinae, and among nearly all the Oedipodinae examined, to transverse disruptive markings in bands and more diffuse mottling.

The operation of all these three tendencies can be traced in the coloration of the British species considered here, and will be further discussed below. It will be helpful to bear them in mind in considering the detailed description of pattern, which now follows.

Description.

First the mode of construction of the colour formulae will be described; then the colour forms found in British species will be listed in terms of these formulae.

Colour Formula.—This will comprise an index of total coloration, and subsequent indices for the various regions of the body, which will add to or modify the general index so far as the details of pattern differentiation require.

The following colour symbols will be used throughout the various indices:—*v* (viridis)—green; *p* (purpureus)—purple; *b* (brunneus)—brown; *n* (niger)—black; *a* (albus)—white; *f* (flavus)—yellow; *s* (stramineus)—straw-coloured; *g* (griseus)—grey.

These colour symbols are always italicised to avoid confusion with symbols for pattern elements. The distinctions between shades of colour are essentially pragmatic and may be varied according to individual needs and purposes; the shades used here have been chosen according to two criteria, namely whether distinction between crucial intermediate cases is at all practicable, and whether the extreme forms of each shade are important enough to justify separation. Green is easily distinguished, but the intergradations of purple, black, yellow and even white with brown are more troublesome, so the intermediate and less clearly defined categories of grey and straw-coloured have been included. The present list is of course not final, but is a suitable general range for the forms described here.

Total Coloration (Symbol *T*).—In this and all the other descriptive categories the insect will be considered in the resting position with elytra closed. The symbol for this category will be *T* (totus), and to it will be appended two colour indices, the first for the general coloration of the dorsum (comprising vertex and occiput, and dorsal surface of the pronotum, and also of the abdomen in the case of brachypterous specimens, e.g. ♀ *C. parallelus*), and the second for that of the sides (comprising face and sides of head, lateral lobes of the pronotum and thoracic pleurae). Examples of the completed term are thus *T v v*, or *T v b*. It should be noted that these differ from two of Rubtzov's named forms (*viridis* and *hyalosuperficies* respectively) in two respects. There is in the first place no implication here that they describe verified homologous forms. Second, Rubtzov's descriptions included elytra, the anal area of which usually shows a correlation with the colour of the rest of the dorsum. However, this correlation is not invariable, and neither is another frequent correlation, viz. of the upper surfaces of the hind femora with the colour of the general sides and of their outer surface with that of the dorsum. Separate terms are therefore used to describe elytra and hind femora, so a complete description, in the simple cases without pattern differentiation, will comprise the three terms for total coloration, elytra and hind femora. A less simple case for the designation of total coloration is that of the form which Rubtzov described as f. *fuliginosa*. This has the upper half of the sides black-brown, the same colour as the dorsum, and the lower half of the sides straw-coloured. It will therefore be designated $T\, n^{n}_{s}$, and will not be classed with true pattern differentiation of the sides, to be described below.

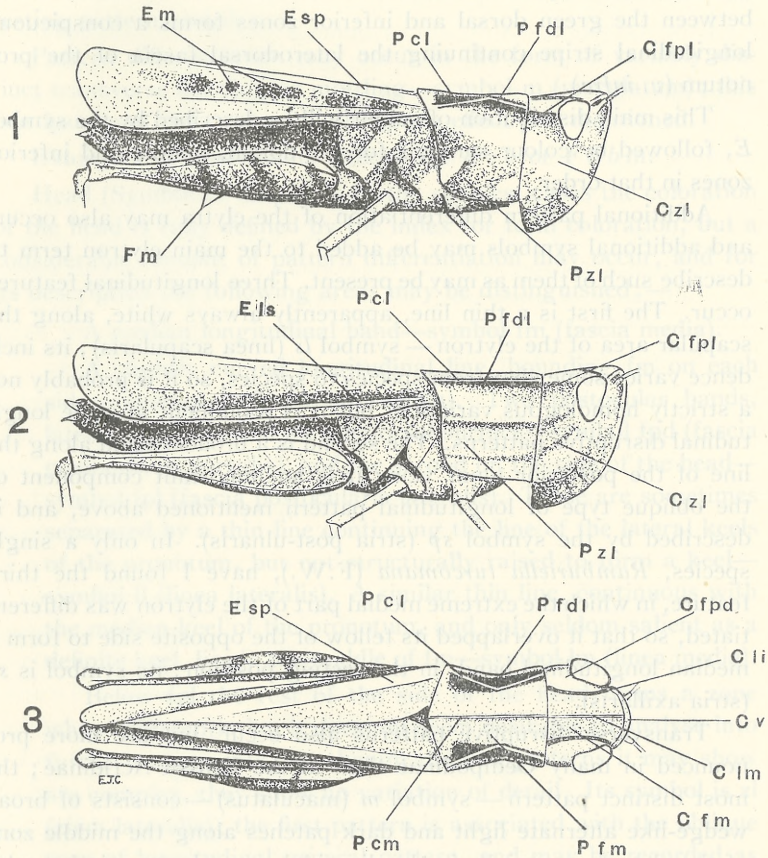
Elytra (Symbol *E*).—A primary distinction may be made between the anal area, or dorsal surface of the elytron, often correlated with the coloration of the dorsum, and the rest of the elytron, or lateral surface in the resting position. With such a distinction, however, it is difficult to fix exactly the boundary between the two parts. In forms *T v b*, with the just-mentioned correlation of elytra and general dorsum colour, of *Stenobothrus lineatus* (Panz.) and *Omocestus ventralis* (L.), or *T a b* of *Chorthippus bicolor* (Charp.), for instance, the boundary between the two colours of the elytra lies along the posterior ulnar vein, while in, e.g., form *T v b* of *C. albomarginatus* the boundary transgresses on to the lateral surface of the elytron in the resting position. I have therefore decided to distinguish three main zones of the elytron, as follows:—

Dorsal zone proper: Limited by the posterior ulnar vein.

Middle zone: Between posterior ulnar and posterior radial veins.

Inferior zone: Below the posterior radial vein.

The term zone is used rather than area, because of the morphological use of the latter. The boundaries show some slight variation, mainly interspecific.



FIGS. 1–3.—1, Side view of oblique type of longitudinal general pattern; 2, side view of horizontal type of longitudinal general pattern; 3, oblique type of longitudinal general pattern seen from above; C, caput; C fm, fascia media; C fpd, fascia postocularis dorsalis; C fpl, fascia postocularis lateralis; C li, linea intermedia; C lm, linea media; C v, vertex; C zl, zona lateralis; E, elytron; E ls, linea scapularis; E m, maculatus; E sp, stria postulnaris; F, femur; F m, maculatum; P, pronotum; P cl, carina lateralis; P cm, carina media; P fdl, fascia dorsolateralis; P fm, fascia media; P zl, zona lateralis.

Further examples of the validity of this distinction between middle and inferior zones are provided by a macropterous female of *C. parallelus*, with the dorsal and inferior zones straw-coloured and the middle zone deep brown, while among foreign species *M. grossus* and *P. alliaceus* have the inferior zone conspicuously pale, as an important component of their characteristic disruptive effect, and *Oxycoryphus compressicornis* (Latr.) and *Paracinema tricolor* (Thunb.) show specimens in which the dark brown middle zone between the green dorsal and inferior zones forms a conspicuous longitudinal stripe continuing the laterodorsal fascia of the pronotum (*v. infra*).

This main distribution of colour will be described by the symbol *E*, followed by colour symbols for the dorsal, middle and inferior zones in that order.

Additional pattern differentiation of the elytra may also occur, and additional symbols may be added to the main elytron term to describe such of them as may be present. Three longitudinal features occur. The first is a thin line, apparently always white, along the scapular area of the elytron — symbol *ls* (linea scapularis); its incidence varies somewhat from species to species, so it is probably not a strictly homologous variation, but it is prominent in some longitudinal disruptive patterns. The second is a broader band along the line of the posterior ulnar vein; it is an important component of the oblique type of longitudinal pattern mentioned above, and is described by the symbol *sp* (stria post-ulnaris). In only a single species, *Ramburiella turcomana* (F.W.), have I found the third feature, in which the extreme medial part of the elytron was differentiated, so that it overlapped its fellow of the opposite side to form a median longitudinal band, in the resting position; its symbol is *sa* (stria axillaris).

Transverse disruptive patterns also occur, but are more pronounced in many Oedipodinae than in the British Acridinae; the most distinct pattern — symbol *m* (maculatus) — consists of broad wedge-like alternate light and dark patches along the middle zone of the elytron, especially in the discoidal area. In association with similar coarse transverse banding of the hind femora it gives a strong disruptive effect in many Oedipodinae. Finer dotting of the whole elytron with darker colour than the general ground-colour is sometimes significant in similar circumstances — symbol *p* (punctatus).

Examples of complete indices for elytra might be *E v b b* or *E b b b* ls *a* sp *s*.

Hind Femora (Symbol F).—In considering the hind femora the term 'upper surface' will be used to include both inner and outer upper surfaces, as morphologically defined, with their boundary keels; if, as sometimes occurs, the inner upper surface tends to the colour of the internal surface, the outer one only will be considered. To the symbol *F* will be appended two colour symbols, the first for the upper surface and the second for the outer surface. The under surface will not be considered, as it is not a component of the resting pattern complex.

Pattern differentiation may occur in the form of variably distinct transverse banding or mottling—symbol m (maculatum); this is a feature of the transverse disruptive effect just mentioned.

Examples of hind femur indices are *F v b* or *F b b* m.

Head (Symbol C—caput).—In the simplest cases the coloration of the head is fully defined by the index for total coloration, but a considerable amount of pattern differentiation may occur, and for its description the following areas may be distinguished:—

A median longitudinal band—symbol fm (fascia media).

A slightly curved longitudinal line, bounding fm on each side—symbol li (linea intermedia). Two postocular bands, lateral to li; the first on the dorsal surface—symbol fpd (fascia postocularis dorsalis), and the second on the side of the head—symbol fpl (fascia postocularis lateralis). These are sometimes separated by a thin line continuing the line of the lateral keels of the pronotum, but not structurally raised to form a keel—symbol ll (linea lateralis). A similar thin line, continuous with the median keel of the pronotum, and only seldom salient as a definite keel, lies in the middle of fm—symbol lm (linea media).

Below fpl the rest of the side of the head forms a zone whose differentiation it does not seem desirable to analyse into further components, as, though the two patterns it may show are complex, they show no variation of detail. Its symbol is zl (zona lateralis); the first pattern is associated with the oblique type of longitudinal general pattern, and may be recorded as zl (o), while the second, associated with the horizontal type of longitudinal pattern, although on the head itself its orientation is rather oblique, is recorded as zl (h). (These two types of pattern are shown in figs. 1 and 2 respectively.)

In a few cases the vertex shows separate colour differentiation—symbol v (vertex).

Not all these areas will be differentiated in the same specimen, and the head is often quite uniformly coloured, but an example of the head index for a complex pattern is C lm *s* li *n* ll *a* zl (o).

The question of side-to-side differentiation of the head in association with a transversely disruptive general pattern hardly arises with the present material; occasionally very faint suggestions of differentiation of the side of the head into anterior and posterior parts appear, but not significantly.

Pronotum (symbol P).—The general plan of differentiation is very similar to that of the head, but there are no invariable correlations between individual areas of each, except in the differentiation of the side pattern as a whole, shown in figs. 1 and 2. The following areas are distinguished:—

A median longitudinal band—symbol fm (fascia media); this is of the same width as C fm, and, though it is usually also of the same colour, occasionally there is a strong colour difference, contributing to a transverse disruptive effect in some foreign species, and contrasting with the more usual longitudinal effect when they are both of the same colour.

Lateral to this is a longitudinal band of variable width—symbol fdl (fascia dorsolateralis); in its greatest width it may extend over all the rest of the dorsum of the pronotum and half-way down the sides, but it may be so narrow as barely to contain the lateral keels. It seems, when differentiated, to be always black; as the lateral keels traverse it they are white, or occasionally purple, and more prominent structurally than in its absence, when they are not usually distinctively coloured. The median keel may also, though less often, be differentiated in structure and colour. The symbols for the keels are cl (carina lateralis) and cm (carina media). The side of the pronotum below fdl shows pattern differentiation of the same sort as C zl (see figs. 1 and 2); its symbol is also zl (zona lateralis), and the two types of pattern are similarly indicated as (o) and (h). The deficiency of the hind part of P fdl with the oblique pattern is noteworthy as suggesting a directing influence of the general type of pattern on the individual component details. The horizontal orientation produced in *C. bicolor* T *a b* nymphs by a rudimentary zl (o) side pattern together with the horizontal boundary line between dorsal and lateral colours of the exposed abdomen also supports this idea of flexibility of individual pattern features. The oblique marking on the thoracic pleurae parallel with that of the lower hind corner of P zl is only prominent with the oblique pattern.

Transverse differentiation is rather more marked than in the head, though never significant enough to contribute to a general pattern in British species. A tendency towards the development of three transverse bands across dorsum and sides is sometimes seen, and may account for a peculiarity of green forms of *Myrmeleotettix maculatus* (Thunb.), in which, when the rest of the side of the pronotum is green, a vertical band comprising about the anterior third of the side is usually deep brown.

An example of a complete pronotum index is P fdl *n* cl *a* zl(o).

Summary of Symbols used

(see also figs. 1, 2 and 3).

Region-Symbol.	Detail-Symbol.	Colour Notation and other comments.
Total — T		Two symbols, the first for dorsum, the second for sides.
Elytra — E		Three symbols, the first for dorsal zone, the second for middle and the third for inferior.
	Linea scapularis — ls Stria postulnaris — sp Stria axillaris — sa	Each followed individually by the appropriate colour symbol.
	Transverse banding—m Fine dotting — p	No colour symbol needed.
Hind femora—F		Two symbols, the first for upper surface, the second for outer side.
	Transverse banding—m	No colour symbol needed.
Head — C	Fascia media — fm Linea media — lm Linea intermedia — li Fascia postocularis dorsalis — fpd Linea lateralis — ll Vertex — v Fascia postocularis lateralis — fpl	Each followed individually by the appropriate colour symbol.
	Zona lateralis — zl	No colour symbol ; pattern symbol only.
Pronotum — P	Fascia media — fm Carina media — cm Fascia dorso-lateralis — fdl Carina lateralis — cl	Each followed individually by the appropriate colour symbol.
	Zona lateralis — zl	No colour symbol ; pattern symbol only.

List of British Forms.

This will consist mainly of forms I have found in my own field work, in the Oxford district and the Reigate district of Surrey, and to these I shall add a rough estimate of their relative abundance as judged from random sampling of colonies. I have supplemented them with a few forms from the British section of the M. Burr collection mentioned above and from the W. J. Lucas collection of British Orthoptera, also at Oxford. I have omitted *M. grossus* from the list, as I have had no personal experience of it, and although there were many British specimens in these two collections it seemed hazardous to try to describe them accurately without any experience of the relation of fresh to dry coloration.

Two points may be noted about the use of the colour formula here. In cases of intermediate shades of colour, or of normally rather wide variability of colour, two colour symbols hyphenated together will be used instead of a single one. Also the symbol ± will be used to indicate variable incidence of minor details; normally it will only apply to the term it immediately precedes, which will be in parenthesis, but when it precedes a group of terms in parenthesis it will indicate variable incidence of the group as a whole.

Sex differences are mainly confined to greater clearness of pattern in the females, perhaps due to their greater size, and to incidence of minor features such as the linea scapularis of the elytra, which is practically restricted to females. Only special cases will be commented on below.

Stenobothrus lineatus (Panzer).

T *v v* E *v n n* ls *a* F *v n-g* or *b n-g* C ll *a* v *a* P fdl *n* cl *a* (abundant).
T *v v* E *v n n* ls *a* F *p n-g* C ll *p* v *p* P fdl *n* cl *p* (occasional).
T *b v* E *b n n* ls *a* sp *s* F *b n-g* C lm *s* li *n* ll *a* P cm *s* fdl *n* cl *a* (occasional).

Omocestus viridulus (L.).

T *v v* E *v b b* F *v v* P fdl *n* cl *a* (abundant).
T *b b* E *b b b* F *b b* P fdl *n* cl *a* (occasional) (characteristic olive-brown).
T *v b* or *v s* E *v b b* (± ls *a*) F *b b* P fdl *n* cl *a* ± (E m F m C lm *s* or *p* zl (o) P cm *s* or *p* zl (o)) (abundant).
T *v p* E *v p p* F *p b* C lm *p* v *p* P cm *p* fdl *n* cl *a* (rare).

Omocestus ventralis (Zett.).

T *b b* E *b b b* F *b b* m ± (E m P fdl *n* cl *a*) (abundant; ♀ only).
T *n-b n-b* E *n-b n-b n-b* F *b b* P fdl *n* cl *a* (abundant; ♂ only).
T *b b* E *b b b* sp *s* m *F b b* m C (± li *n*) zl (o) P fdl *n* cl *a* zl (o) (frequent).
T *v b* E *v b b* ± m F *b b* ± m C lm *s* ± zl (o) P cm *s* cl *a* fdl *n* ± zl (o) (frequent; ♀ only).
T *a-s b* E *a-s b b* F *b b* m C li *n-b* fpd *b* P fdl *n* cl *a* (1 specimen; Burr collection).

Myrmeleotettix maculatus (Thunberg).

T *v v* E *b b b* m (± *p*) F *v b* m (occasional).
T *v v* E *b b b* m F *v b* m P fdl *n* cl *a* ± (E sp *s* C zl (o) P cm *s* zl (o)) (frequent).
T *b b* E *b b b* m (± p) F *b b* m (frequent).
T *b b* E *b b b* m F *b b* m C (± li *n*) P fdl *n* cl *a* ± (C lm *s* zl (o) P cm *s* zl (o)) (frequent).
T *b-n* $\frac{b\text{-}n}{g}$ E *b-n b-n b-n* m F *b b* m (1 specimen only).
T *a-s b* E *a-s b b* m F *b b* m C li *n* fpd *n-b* P fdl *n* cl *a* (1 specimen; Burr collection.
T *b v* E *b b b* m F *v b* m P fdl *n* cl *a* ± (C fm *v* P fm *v*) (occasional).
T *p p* E *p b b* sp *s-p* m F *b b* m P cl *a* fdl *n* ± (C zl (o) P zl (o)) (rare).
T *p v* E *p b b* (± sp *p*) m F *v p* m C all *v* P fdl *n* cl *a* ± zl (o) (occasional).
T *p b* E *p b b* (± sp *p*) m F *b b* m P fdl *n* cl *a* (occasional).

Chorthippus bicolor (Charp.).

T *v v* E *b b b* p F *v v* (1 specimen only).
T *b b* E *b b b* (± p) F *b b* (± m) ± (C zl (o) P zl (o)) (frequent) (=Vorontzovskii's v. *robusculus*?).
T *b b* E *b b b* (± ls *a*) m F *b b* m P fdl *n* cl *a* ± (C zl (o) P zl (o)) (abundant).
T *b b* E *b b b* ls *a* sp *s* m F *s-b b* m C (± li *n-b*) zl (o) P cm *s* fdl *n* cl *a* zl (o) (frequent; see figs. 1 and 3 for this type of pattern).
T *p p* E *p p p* F *p p* ± (P fdl *n* cl *a*) (rare).
T *n n* E *n n n* F *s s* m (occasional).
T *v b* E *v v b* m F *b b* m C li *b* fpd *s* ± (C zl (o) P fdl *n* cl *a* zl (o)) (frequent).
T *p b* E *p p b* m F *b b* m ± (C zl (o) P zl (o)) (frequent).
T *p b* E *p p b* m F *b b* m P fdl *n* cl *a* ± (C lm *s* zl (o) P zl (o)) (frequent).
T *s-a b* E *s-a b b* F *b b* m C li *n* fpd *n-b* P fdl *n* cl *a* (occasional).
T *n s* E *n n n* F *s s* m (occasional) (=Vorontzovskii's v. *nigrosuperficies*?).
T *g s* E *b b b* m F *b b* or *g g* C zl (o) P fdl *n* cl *a* zl (o) (occasional).

Chorthippus parallelus (Zett.).

T *v v* E *v v v* F *v v* or *v b* or *b b* or *p p* or *v p* C (± fpl *n*) (abundant; ♂ elytra often dull, nearly E *v b b*).
T *b b* E *b b b* F *b b* ± (C zl (o) P zl (o)) (frequent).
T *b b* E *b b b* sp *s* F *b b* (± m) C lm *s* zl (o) P fdl *n* cl *a* zl (o) (occasional).
T *p p* E *b b b* F *p p* C li *n-b* zl (o) P fdl *n* cl *a* zl (o) (rare).
T *v b* E *v v v* F *b b* C (± fpl *n*) ± (C zl (o) P zl (o)) (abundant)
T *v p* E *v v v* F *p p* C (± fpl *n*) (frequent)
} (♂ elytra dull, nearer E *v b b* or E *b b b*).
T *b v* E *b b b* (± ls *a*) F *v b* (abundant).
T *b v* E *b b b* (± ls *a*) sp *s* F *v b* C (± lm *s-a*) li *n-b* (± fpl *n*) P fdl *n* cl *a* (frequent) (E *s n-b s* in a few specimens, especially a macropterous ♀, approaching the *M. grossus* type of pattern).
T *p v* E *b b b* or *p b b* (± ls *a*) F *v p* C (± fpl *n*) (frequent).
T *s-a v* E *s-a b b* (± ls *a*) F *v b* C (± li *n-b*) (± fpl *n*) (occasional).
T *s-a b* E *s-a b b* F *b b* (± m) C li *n-b* ± (P fdl *n* cl *a*) ± (C zl (o) P zl (o)) (occasional).

Chorthippus albomarginatus (De Geer).

T *v v* E *v v b* F *v v* C (± fpd *s*) (occasional).
T *b b* E *b b b* F *b b* C li *n-b* (abundant) (± E ls *a*, confined to the ♀).

T *b b* E *b b b* (± ls *a*) (± p) F *b b* C li *n-b* zl (h) P cm *s* or *n-b* fdl *n* cl *a* zl (h) (frequent) (see fig. 2 for this type of pattern). (Salience of P cm, both here and in *C. bicolor,* is not so often correlated with light colour as is that of P cl, which is nearly always white when salient, except in male *C. albomarginatus.*)

T *v b* E *v v b* (± ls *a*) F *b b* C (± fpd *s*) ± (C zl (h) P cl *a* zl (h)) (frequent).

T *b v* E *b b b* (± ls *a*) (± p) F *v b* ± (P fdl *n* cl *a*) (occasional).

T *p v* E *p p b* ls *a* F *v p* (2 specimens only).

T *f b* E *f f b* (± ls *a*) F *b b* ± (P fdl *n* cl *a*) (frequent).

T *n* $\frac{n}{s}$ E *n n n* ls *a* F *b-s b-s* (1 specimen only) (= Vorontzovskii's v. *fuliginosus* Ivan).

Gomphocerus rufus (L.).

T *b b* E *b b b* F *b b* (± m) ± (C zl (o) P zl (o)) (abundant).

T *b b* E *b b b* (± p) F *b b* (± m) P fdl *n* cl *a* (abundant).

T *b b* E *b b b* sp *s* F *b b* m C lm *s* li *n-b* zl (o) P cm *s* fdl *n* cl *a* zl (o)) (frequent) (see figs. 1 and 3).

T *p p* E *b b b* F *p p* m C li *b* P fdl *n* cl *a* (1 specimen only).

T *n n* E *n n n* F *s s* m (occasional).

T *s-a b* E *s-a b b* F *b b* (± m) C li *n-b* P fdl *n* cl *a* ± (C zl (o) P zl (o)) (frequent).

In spite of the detailed nature of this list, much variable incidence of minor features has not been recorded; examples are the details of incidence of purple or white keels in *S. lineatus,* or of occasional cases of mixed colours on the dorsum, such as the following form of *C. parallelus*:—

T *v v* E *b b b* F *v p* C fm *p* li *p* fpd *p* P cm *p*.

A fairly general tendency which it was also not possible to record in detail in the list is that towards a lighter shade on the dorsum than on the sides, shown particularly by dark brown and dark grey forms of *C. bicolor, M. maculatus* and *O. ventralis,* independently of the tendency of the sides to be lighter towards the ventral surface.

Discussion.

The tendency to the three types of disruptive coloration already mentioned is evident in the British fauna. A more or less uniform distribution of colour, with little pattern differentiation, is shown by a large proportion of *C. parallelus* and *C. albomarginatus*; this may be correlated with relatively mesophilous habit, while species with a higher proportion of forms with pattern developed tend to be more xerophilous, e.g. *C. bicolor, M. maculatus* and *G. rufus*; further, pattern differentiation is more complete among brown forms than green ones, and Rubtzov (loc. cit.) has shown that there is a higher proportion of brown forms in the drier habitats of *C. albomarginatus.* The first and simplest type of disruptive effect, that of *M. grossus,* is produced by the longitudinal dark line of C fpl, P fdl, and the proximal part of the middle zone of the elytron, with the superior zone of the elytron making a pale stripe below this; this effect, however, is not as striking in *M. grossus* as in the foreign *P. alliaceus*, as the general colour of *M. grossus* tends to be dark and somewhat irregularly mottled. The oblique type of longitudinal effect (see figs. 1 and 3) is most completely developed in brown specimens of *C. bicolor* and *G. rufus*, which are described by the formula:—

T *b b* E *b b b* ± ls *a* sp *s* ± m F *b b* m C ± lm *s* li *n* zl (o)
P cm *s* fdl *n* cl *a* zl (o).

Even in this well-developed form there is still some variability of minor features, and this variability is emphasised by the various forms transitional to the complete effect in *C. bicolor, G. rufus, M. maculatus, C. parallelus, S. lineatus, O. viridulus* and *O. ventralis*. In relatively few of these is a disruptive effect very conspicuous, but the relation of their various fragmentary features to the complete pattern justifies considering them as potential or incipient disruptive patterns. The horizontal type of longitudinal pattern is shown only by *C. albomarginatus* among British species, and is probably to be correlated with parallel or less strongly angled keels of the pronotum, whose direction is followed by the white scapular line of the elytra and the horizontal orientation of the side pattern (see fig. 2). It is never very strikingly disruptive in *C. albomarginatus*, but specimens in the Burr collection, e.g. of *Euchorthippus pulvinatus* (F.W.) or *E. albolineatus* (Lucas), have it more clearly developed. I have only found it in brown forms of *C. albomarginatus*, in contrast to the oblique type of pattern, which is found in green and purple forms of *M. maculatus* and purple ones of *C. bicolor*, as well as in brown ones. With both oblique and horizontal patterns the most important points of differentiation are first P fdl and cl, then features of the elytra, and then the side pattern. A conspicuous variant of the oblique type is the form of *C. bicolor* and *G. rufus* with pale C fm, P fm and dorsal zone of the elytra

Transverse effects are not developed in British species to the exclusion of longitudinal ones, as they are in many Oedipodinae, in which the mottled effects of elytra and hind femora are accompanied by a tendency to rough outlines and coarseness of detail; this is probably correlated with dry stony habitats, an idea supported by the frequent occurrence of quite strong mottling of elytra and hind femora in *C. bicolor* and *M. maculatus*.

The main feature of the list, however, is the considerable variability of most species. This, coupled with the relatively flexible habitat requirements of most (*M. grossus* is a conspicuous exception), suggests that the British species provide good examples of potential adaptability to a wide range of environmental conditions, and therefore good material for observing the effects of these conditions on the various tendencies to specialisation of coloration which can be seen in Acrididae in general. I have indeed designed this system more especially with a view to work correlating the various features of colour and pattern with habitat, and this has incidentally meant that a number of features irrelevant to this point of view have had to be ignored. For instance, probably many details of genetical interest have been omitted, and only one aspect of adaptive coloration has been considered, namely procryptic effects at rest; another obvious aspect is that of flash-colour in flight, covering the bright under-wing colour of Oedipodinae and possibly the bright red colour of the tip of the abdomen or the hind tibiae; however, a system can hardly be derived to do justice to all these at once, and coherence and relative simplicity have had to be preferred to comprehensiveness.

Summary.

(1) A system of recording the resting coloration of Acrididae by means of a colour formula is described. It is based on the British species of Acrididae, and so is more particularly applicable to Acridinae, and it interprets the coloration in terms of tendencies to disruptive pattern.

(2) The colour variation of British Acrididae is recorded in terms of this system.

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Corrigenda.

On pages 94 and 96 the following symbols should be in Roman type and not italics: T, E, ls, sp, sa, m, p.

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