The Variable Coloration of the Acridoid Grasshoppers

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As he smoked, his legs stretched out in front of him, he noticed a grasshopper walk along the ground and up on to his woollen sock. The grasshopper was black. As he had walked along the road, climbing, he had started many grasshoppers from the dust. They were all black. They were not the big grasshoppers with yellow and black or red and black wings whirring out from their black wing sheathing as they fly up. These were just ordinary hoppers, but all a sooty black in colour. Nick had wondered about them as he walked, without really thinking about them. Now, as he watched the black hopper that was nibbling at the wool of his sock with its fourway lip, he realized that they had all turned black from living in the burned-over land. He

realized that the fire must have come the year before, but the grasshoppers were all black now. He wondered how long they would stay that way.

Carefully he reached his hand down and took hold of the hopper by the wings. He turned him up, all his legs walking in the air, and looked at his jointed belly. Yes, it was black too, iridescent where the back and head were dusty.

He tossed the grasshopper into the air and watched him sail away to a charcoal stump across the road.

Big Two-hearted River
(Ernest Hemingway, 1963, with permission of the publishers)

I. DEFINITIONS, TERMINOLOGY, AND TAXONOMY

Coloration includes both *colour,* which describes the reflectance of the pigments of a given area, and *pattern,* which describes the distribution of pigments. *Variable* coloration in this review is understood to describe the possibility of different colorations existing in different individuals of the species who are otherwise similar in age, sex, and maturational state. It excludes differences associated with regular sexual dimorphism, sexual maturation, or changes in coloration characteristic of different stadia, but invariable within those stadia. For example *Phyteumus purpurascens* (Pyrgomorphidae) has a typical and different coloration for almost every one of its seven stadia, but all individuals of the same age and sex are similar; this is not an example of variable coloration. In other words, only *simultaneous polymorphism* is here considered. The polymorphism may be due to differences in the genotype or to phenotypic differences derived by the interaction of a given genotype with varying environments. In the grasshoppers, variation of this sort is usually long-term, there being almost no short-term colour change. The exception to this is the temperature-dependent colour change described by Key and Day (1954a, b) from *Kosciuskola* (Catantopinae) and a few other genera, and this is excluded from the discussion below.

The Acridoidea are here understood and classified as by Uvarov (1966, p. 397). Most of the specific examples cited are European or African forms, and authors for generic or specific names are not given, as these can be obtained from either Uvarov (1966) or Dirsch (1964). The names of families and subfamilies given after cited genera are abbreviated after the following scheme:

Pyrg.	Pyrgomorphidae	Euryph.	Euryphyminae
Hemiacr.	Hemiacridinae	Eypr.	Eyprepocneminae
Trop.	Tropidopolinae	Catant.	Catantopinae

Ox.	Oxyinae	Acrid.	Acridinae
Copt.	Coptacridinae	Oed.	Oedipodinae
Cyrt.	Cyrtacanthacridinae	Trux.	Truxalinae
Callipt.	Calliptaminae	Gomph.	Gomphocerinae

thus, *Heteracris vinaceus* (Eypr.).

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II. INTRODUCTION–VARIABLE COLORATION AND THE NATURAL HISTORY OF GRASSHOPPERS

It is common knowledge, among naturalists and entomologists in temperate regions, that the coloration of acridoid grasshoppers is very variable. This usually reflects the realization that coloration is not an adequate guide to the taxonomy of temperate grasshoppers, in the way that it is for temperate Lepidoptera. To some extent this prevalent view reflects the preponderance in the North Temperate of Oedipodine and Gomphocerine genera, which are particularly variable. In all subfamilies there are, however, species which show little or no variation, and in many divisions, particularly among the tropical fauna, there is a preponderance of invariant species. The Pyrgomorphidae, Lentulidae, Hemiacridinae, Coptacridinae and Eyprepocnemidae of Africa afford examples of such mainly invariant groups. The majority of grasshopper species pass through at least two different colorations in their life-history, often changing from one to the other at the final moult, and the larval and adult colorations, as would be expected from evolutionary theory, often show divergent specializations. Such divergence includes variation as here understood; for example, most Cyrtacanthacridinae have larvae which show one or more sorts of simultaneous polymorphism, especially green/brown polymorphism and occasionally phase polymorphism; the adults are much more invariable, losing the green/brown polymorphism completely in most cases and showing phase effects on coloration to a much reduced extent.

The selection pressures which act in coloration are unendingly diverse, and the balance between variable and invariable coloration in any given life-stage of grasshopper species must be dictated by their resultant. It is, however, possible to list common associations between variant and invariant coloration and various other

specializations which the different species show. These associations are observable empirically, but would also be expected on theoretical grounds.

Variable coloration is associated with

(i) Geophilous habit
(ii) Grassland habitats
(iii) Temperate or alpine habitats
(iv) Phase transformation
(v) Acoustic epigamic displays.

The first two of these result in environments in which the prevailing colour of the background is subject to seasonal change or local variation, and the variation found in the acridoid inhabitants is such as to make them predominantly cryptic. Grasslands change seasonally not only from green to brown with the wet and dry seasons, but are also subject to grass fires which transform the environment to predominantly black, while the substrate colour available to a geophilous species changes sharply with local geology and humidity. Relatively few species of grasshopper inhabit temperate and alpine zones; one presumes that interspecific competition is less and each is found in a greater diversity of habitats than in the lowland tropics. The capacity for variation is accordingly of greater selective value. The colour variation brought about by phase transformation differs sharply from the first three categories, in that it seems to make the individual less rather than more cryptically coloured. The selective advantage of this is obscure, but it seems possible that conspicuous coloration of gregarious hoppers facilitates visual responses which make possible aggregation into bands and their subsequent maintenance. Acoustical interspecific communication reduces the importance of species-specific coloration and of associated visual displays, and thus the selection pressure against variable coloration.

Invariant coloration is associated with a complex of factors which complement the above. These are:

(i) aseasonal or otherwise colour-stable habitats, including especially tropical wet forest and swamp, and excluding most other grasslands;
(ii) intraspecific visual signals, including epigamic displays and patterns promoting social cohesion in obligately social forms;
(iii) interspecific visual communication, including aposematic and possibly mimetic coloration, "flash" coloration of rear wings, etc.

It is obvious that many of these factors are either not strictly independent, or if they are, are not exclusive. Most grasshoppers have coloration elements which can be attributed, in an evolutionary sense, to several of the factors listed above, and particular combinations are especially common in certain habitats. This is perhaps best illustrated by example, a number of which are given below.

a. *Cryptic grassland forms.* These genera are usually elongate slender animals, often sluggish or slow moving, sometimes with reduced or absent wings. They show more or less striking resemblances to the plants on which they live. They usually have a well-developed green/brown polymorphism and a rapid and effective homochrome response to black backgrounds, but lack the orange pigment homochrome systems which are associated with a geophilous habitat. Some (e.g., *Acrida, Cannula*) have pattern polymorphism, probably allelomorphic, which results in either longitudinal striping (disruptive coloration), or symmetric or asymmetric blotching with yellow pigment in the black homochrome form, which gives a striking resemblance to charred grass fragments. Most have well-developed acoustical signals, either stridulatory as in the relevant Truxalines, Gomphocerines and Hemiacridines, or by mandible clicking, as in *Acrida.* Where there are also visual displays, the associated specialized colour areas are confined to areas which are normally hidden in the resting position of the animal, such as the blue and red patches on the inner surface of the metathoracic femora of *Mesopsis laticornis* (Gomph.). In species which fly, the hind wings often provide a flash colour as in *Acrida* (Acr.) and *Truxalis* (Trux.). Other representative genera are *Amphicremna, Machaeridia, Cannula* (Acr.); *Mesopsera* (Catant.).

As exceptions to the above generalizations it may be noted that the Hemiacridines *Leptacris* and *Acanthoxia* apparently lack the green morph.

This group makes an interesting contrast with the small number of genera typical of a very different grassland habitat, that of tropical swamp. These species are more active and less morphologically specialized for a cryptic appearance. Their environment is almost completely stable in colour. They themselves show very little variation. They are green, without the brown morph; show no homochrome response to background; and often have an invariant linear pattern. Examples are seen in *Oxya hyla* (Ox.), and *Paracinema tricolor* (Oed.).

b. *Gramnivorous geophilous forms.* These show no extreme morphological specializations, but are perhaps the most prone to coloration polymorphism. They show the full range of homochromic responses: black and orange pigment systems, a well-developed green/brown polymorphism, and often considerable allelic polymorphism, involving both specific features such a metathoracic tibial colour and the whole patterning of the individual. They are often extremely cryptic. Associated with this they have well-developed stridulatory and other acoustic mechanisms; where these are supplemented by visual displays at close quarters, the displays are either purely dynamic, or involve colours not normally visible, such as the back wings. The group is most typically represented by the Oedipodinae; the genera *Chortoicetes, Gastrimargus, Locusta, Locustana, Oedipoda,* and *Oedaleus* account for most of the experimental work on environmentally controlled colour variation. Many of the Gomphocerinae could also be included, though the group is a much more diverse one and less specifically geophilic in its colour adaptations. The best known members of this group are the temperate, rather unspecialized, genera such as *Chorthippus,* where variation is predominantly genetic. The extreme colour variation of Afroalpine forms, such as the related *Dnopherula werneriana,* or of *Coryphosima amplificata* and *Uganda kilimanjarica* (Acrid.), all of which are dominant species with few competitors over large areas of montane grassland, is probably of the same type. The variation seen in tropical lowland species of the same genera is less.

c. *Geophilous forms eating broad-leaved plants.* This is not a large category, but it makes an interesting contrast with the above. Examples are *Chrotogonus* (Pyrg.) and *Trilophidium* (Oed.) and possibly *Gemeneta* (Catant.). These animals are almost never seen on any substrate other than bare earth; they feed on the edges of low-growing herbs, while still remaining on the earth themselves. They give excellent homochrome response to background with both the black and orange pigment systems, but to my knowledge lack completely any green morph.

d. *Wingless high alpine forms.* A number of genera of different families living in the Afroalpine habitat have lost or greatly reduced their wings. The larvae fulfil the expectation that they will be of variable coloration, in view of their relatively uncolonized habitat. Thus the larvae of *Occidentosphena* and *Parasphena* (Pyrg.) and of *Pezocatantops* (Catant.) are green/brown polymorphic; in *Parasphena* they are additionally able to make homochromic response to

background with black, orange and possibly purple pigment systems, while *Pezocatantops* sometimes also assumes the quite different adult coloration in the mid-larval stadia. As adults, however, they are invariable with bold patterns and quite bright colours. Presumably visual signals are important in mating, as none stridulate. The brachypterous subalpine and high montane species of *Phymeurus* (Euryphyminae) are similarly silent and use visual epigamic displays, though in this case associated coloration is confined to the inner surface of the metathoracic femora. They differ from the preceding genera in several ways. All stages are dully coloured and obscurely patterned in grey and black and relatively invariable, though undoubtedly cryptic.

e. *Wingless tropical forest forms.* These are a strikingly uniform group, derived by convergence from many different subfamilies. They tend to be brachypterous or apterous, forb-feeding, scuttlers rather than jumpers, brilliantly and invariantly coloured, and having visual, not acoustic, epigamic displays. They are perhaps at their best in wet lowland secondary forest in Africa; a selection of flightless forms from there would include *Pterotiltus* (Ox.); *Cyphocerastis, Paracoptacra, Ruwenzoracris* (Copt.); *Heteracris* spp. (Eypr.); *Serpusia, Auloserpusia* and related genera (Catant.); and *Odontomelus* (Acrid.). Similarly invariable brightly coloured forms from the same forests, but having functional wings, extend both the genus and family lists; typical examples are *Heteracris vinaceus* (Eypr.); *Parapropacris rhodopterus, Orbillus coeruleus* (Catant.); and *Pachynotacris amethystinus* (Cyrt.). The edges of montane forests also contain populations of flightless species in many ways intermediate between this group and the last, such as *Eyprepocnemis montigena* (Eypr.), *Kinangopa jeanneli, Ixalidium haematoscelis,* (Catant.), *Coryphosima* sp. A (Moroto) (Jago, in prep.) (Gomph.).

f. *Aposematic coloration of distasteful species, and other invariant patterns with a non-sexual signal function.* Some grasshoppers have patterns and colour combinations which are either glaringly conspicuous or are conventionally associated with a mimetic assemblage, such as black and yellow stripes or bands. Some of the brightly coloured forest species of the preceding group may possibly be distasteful, but there is no evidence of this. The only grasshoppers known to be habitually poisonous or distasteful are some members of the Pyrgomorphidae and Romalinae, and those that have been investigated (e.g. *Poecilocerus, Phymateus* and related genera) derive their active constituents from their food plants

(Rothschild and Parsons, 1962; van Euw *et al.*, 1967; Reichstein, personal communication and 1967). Not all of these are brightly coloured, and the provenly distasteful *Phymateus* group are not conspicuously coloured or patterned at all as adults, though when molested they display flash coloration; *Dictyophorus* has brilliant orange and black stripes as a larva but is totally obscure, apart from its pink back wings, as an adult; and some of the most brilliantly coloured are not known to be poisonous at all. In several of these cases it seems that the coloration may serve signal functions other than or additional to the aposematic, such as group cohesion; see Rowell (1967a) for a discussion of these.

III. GENETIC FACTORS

Much of the variable coloration of the Acridoidea is at least partially determined by environmental factors, and shows phenotypic lability more or less independently of genotype. The majority of the experimental work concerns this type of coloration, and this review is primarily devoted to it. However, it is obvious that the limits of this phenotypic lability are set by the genotype; further, some examples of simultaneous polymorphism are purely or largely genetic in character, and the environment influences them little or not at all. Examples of both of these genetic influences are given below.

A. GENETIC POLYMORPHISM

The relatively small amount of experimental work which has been performed indicates considerable differences in the extent to which the phenotype is modifiable by environmental factors, and it seems that this condition is commonest among the Acridoidea. In the other groups the indications are that genetic polymorphism is the more important.

The extreme case of a polymorphism with an exact correspondence between genotype and phenotype appears among the Tettrigidae. Nabours (1929) bred *Paratettix texanus* and *Apotettix eurycephalus* for over 20 years and more than 60 generations. The species both show an extraordinary range of colour and pattern composed of defined forms, and which does not form a graded series. In *Paratettix* at least 18 factors were isolated influencing colour and

pattern. Fisher (1930, 1939) showed from these data that the diversity of the genotype was maintained by selection against the homozygous dominant; the homozygous recessive was not so affected. Further, in wild though not in caged populations, there was strong selection pressure against the pairing of more than one heterozygote in one individual. No environmental effects were found influencing coloration: "neither excessive humidity, temperature, aridity, acidity, salinity, sunlight through glass or direct, darkness, color of soil, food, excreta, starvation, fungus disease, parasitism, nor any other observable feature of the environment has ever changed color pattern to any appreciable extent" (Nabours, 1929). Comparable situations exist in other Tetrigid genera (see, e.g., Good, 1941, *Tettigidea parvipennis*) and in the Eumastacid Morabine grasshoppers (e.g. Lewontin and White, 1960). They have been important in the development of the concept of the super-gene.

Relatively little is known of the control of colour polymorphism in the Grylloidea or Tettigonioidea. Within the latter a number of phytophilous families (e.g. the Phaneropteridae, Tettigoniidae and Conocephalidae) include genera in which there is well defined green/brown polymorphism, the basis of which is largely unknown. Verdier (1958) produced evidence that *Barbistites fischeri, Ephippiger provincialis,* and *Orphania denticauda* and *O. scutata* reared in captivity were green in isolation, but brown when crowded; this is especially unexpected in *E. provincialis,* as a green form is unknown in the wild. The constancy of the green and brown proportions in the E. African races of *Homorocoryphus nitidulus* (Owen, 1965; Karuhize, 1968) argues either a genetically controlled polymorphism or a remarkably consistent environment; individuals of this species, reared in high humidity, show no colour differences associated with density (Rowell and Mukwaya, unpublished). In addition, many of these polymorphic tettigoniid species show occasional purple coloration, affecting either morph. In at least two species this is controlled by a single dominant allele (*Amblycorypha oblongifolia,* Phaneropteridae, Hancock, 1916; *Homorocoryphus nitidulus,* Conocephalidae, Rowell and Mukwaya, unpublished).

Data on genetic polymorphism of the Acridoidea themselves are disparate and uncommon. It is clear that such polymorphisms are frequent, if not well known. For example, many genera ((e.g. *Truxalis* (Trux.) and *Morphacris* (Oed.)) are polymorphic in the colour of their hind wings, and the different geographical populations vary markedly in the relative frequency of these forms.

In such widely distributed species, colour and pattern may vary considerably over the range, and on occasion it has been noted that these differences persist for generations under standard culture conditions, indicating genotypic differences (*Locusta pardalina*, Nolte, 1962; *Gastrimargus africanus*, Rowell and Hunter-Jones, unpublished). King and Slifer (1955), investigating the variation in colour of the hind tibia of *Melanoplus sanguinipes* (Catant.) showed that red colour is due to a dominant autosomal gene, and blue to its recessive allele, though other genes modify these effects, mostly in dilution of the colour. Brett (1947) had previously demonstrated that the proportions of these colours in a population and their intensities are also modifiable phenotypically by food plant, and slightly by temperature and humidity. Many genera include a form (=*forma porphyrica* of Rubtzov, 1935) in which part of the animal, mostly the dorsal areas of vertex, pronotum and elytra, is purple; European examples are given by Vorontskovskii (1929), Rubtzov (1935), and Ramme (1951) from the Gomphocerinae, and other subfamilies showing this trait include the Hemiacridinae (*Spathosternum*), Oedipodinae (*Aiolopus*) and Acridinae (*Duronia, Roduniella, Gymnobothris*, etc.) in Africa. In *Aiolopus thalassinus* this form appears to be controlled by a single dominant allele (Rowell, unpublished observation) as in the tettigoniids noted above, and this may well be the general case.

Collectors are familiar with a number of very rare but reproduceable colour variants, which are probably due to recurrent mutation. Thus in the related genera *Humbe, Gastrimargus* and *Heteropternis* (Oed.) the normal pronotal coloration may be replaced by a uniform pale yellow, pink, or white; in *Acanthacris ruficornis* (Cyrt.) the dorsal pronotum is occasionally dark green instead of sienna; *Cyphocerastis* sp. A (Jago, in preparation) (Copt.) normally has a clear greenish-yellow pronotum, but occasionally wild individuals with this colour replaced by pink are found. The incidence of these forms has not been properly determined, but in all these examples is certainly well below 0.1%. Substantiated cases of such mutation are the albino forms reported for *Schistocerca gregaria* (Cyrt.), *Melanoplus sanguinipes* (Catant.) and *Locusta migratoria* (Oed.) (Hunter-Jones, 1957; Putnam 1958; Verdier, 1965, Nolte, 1968), and the melanic form of *S. gregaria* (Volkonsky, 1938).

At a greater level of complexity, Byrne (1962, 1967a, b) showed that nine taxonomically recognized forms (Key, 1954) of *Chortoicetes terminifera* (Oed.) corresponded to the possible

combinations of four alleles (i.e. four homozygotes and six heterozygotes), two of which gave an indistinguishable phenotype. These factors affected only the melanic pattern and part of the brown pigment system, probably the ommochrome fraction. In high humidity the animals developed green pigment, and this masked or excluded the other pigments. White (1968) describes a bilateral gynandromorph of *Valanga irregularis* (Cyrt.) which expressed two of the six pattern polymorphs of this species. Together with the naturally occurring proportions of the different forms in different localities, this suggests genetic control of colour and pattern in this species. Finally, it seems likely that the best known Gomphocerine genera, such as *Chorthippus*, may derive their bewildering variation almost entirely from the genotype, after the manner of the tettrigids. There is strictly only one genetic experiment. In *Chorthippus parallelus* Sansome and La Coeur (1935) were able to separate ten factors affecting colour and/or pattern. Six of these inhibit the expression of at least two nonallelomorphs, and in addition at least two others interfere with the expression of several other genes. The authors point out that one phenotype may thus correspond to a comparatively large number of genotypes, and that by this epistasy the species is able to react readily to different habitats (i.e. through selection) and yet remain fairly uniform in one habitat. The authors do not attach much importance to phenotypic variation. Rubtzov (1935) confirmed this belief with field observations and laboratory experiments on related Gomphocerine species, including *C. albomarginatus*; with the possible exception of social stimuli derived from crowding, environmental stimuli appeared unimportant. Similar views were expressed by Richards and Waloff (1954) after a field study of *C. brunneus* and other British Gomphocerines; variation appeared to reflect a stable genetic polymorphism, different in each population, and to be relatively unaffected by environmental fluctuations other than via long-term fecundity or differential survival of some forms. It is, however, likely that *Chorthippus* (Burton, 1960) does have a homochrome response to low albedo (see Section IIIA).

B. GENETIC MODIFICATION OF PHENOTYPIC POLYMORPHISM

Of the various phenotypic responses to environmental stimuli, the green/brown polymorphism is known also to be affected in a number of species by the genotype of the individual. Thus in the

Oedipodinae green forms are always commoner among males than females in some genera, regardless of experimental conditions (e.g. *Humbe tenuicornis,* Walter, 1965; *Gastrimargus africanus,* Rowell, 1967b, 1970; *Heteropternis couloniana,* Rowell, unpublished), while in other genera the opposite is the case (*Chortoicetes terminifera,* Byrne, 1962; *Ailopus thalassinus,* Walter, 1965; *Locustana pardalina,* Nolte, 1963). The probable basis for such distributions is provided by the work of Stehr (1959) on the similar, but environmentally insensitive, polymorphism of haemolymph colour in the lepidopteran genus *Choristoneura.* Both protagonistic and suppressor loci for the green colour were found, and the latter was situated on the sex chromosome.

It was noted above that in *Chortoicetes* the environmental response to high humidity is a green pigmentation which obscures the genetically determined patterning. However, there is also the opposite interaction. Not all the genetic variants are equally likely so to respond to high humidity, and Key (1954) considers that the majority of wild green forms represent the form *nigrovirgata,* which is the most susceptible to the green morph.

The example of *Chortoicetes,* in which a coloration element which is primarily controlled environmentally is also influenced genetically, is presumably typical. Other known cases are seen in the locusts. *Locustana pardalina* responds to humid environments when solitary with the green form of the green/brown polymorphism. The ability to respond to the environment in these ways is selectable, and strains of different capacity can be separated (Nel, 1968). Similarly, Hunter-Jones (1958), Nel (1967a, b) and Fuzeau-Braesch (1961) have shown that the propensity for responding to high density with gregarious phase coloration can be readily selected for in *Schistocerca gregaria, Locusta* and *Locustana,* and in the Gryllid *G. bimaculatus.* Ultimately such genetic differences in the ability to respond differentially to environmental stimuli distinguish most grasshoppers from the locusts and other species which respond to the social environment by change, not only in colour, but often in behaviour and other aspects of their physiology as well.

IV. ENVIRONMENTAL FACTORS

The variable coloration of the acridids that are phenotypically polymorphic consists of the interplay of a number of basically independent pigment systems. These are here defined phenomeno-

logically in terms of the colours they produce, and the stimuli they respond to, rather than as metabolic processes. A specific pigment metabolism may be influenced by more than one of these systems and a system may include more than one pigment; this is treated further in Section VI. The evidence for these separate pigment systems derives from the observation that they can vary independently in the population, from experimental work on the adequate environmental factors and the physiological mechanisms which they excite, and from pigment chemistry. The pigment systems here recognized are as follows:

(a) The black pigment system.
(b) The orange pigment system, which may itself be a heterogeneous category, and mediates colours of yellow to reddish orange.

Together (a) and (b) mediate the homochrome responses to background colour.

(c) The green/brown polymorphism and the pigments which mediate it.
(d) Phase coloration, in those forms which have a coloration characteristic of gregarious phase.

Though basically independent, these systems do interact, and these interactions will be returned to below.

A. THE HOMOCHROME RESPONSE TO BACKGROUND: THE BLACK AND ORANGE SYSTEMS

1. Extent and Occurrences

A majority of geophilous and many gramnivorous grasshopper species resemble the general coloration of their background. Further, this resemblance holds when the species extends over a variety of differently coloured habitats, and also when the habitat is prone to seasonal or irregular colour change. The best known case of the latter is the observation that grasshopper populations of recently burnt vegetation are predominantly black.

The explanation of these observations must lie among the following:

(i) the population is variable in coloration. Matching is achieved by differential predation;
(ii) the population is variable in coloration, and individuals select habitats matching their own colour;

(iii) individuals change colour to match the background: i.e. they make a homochrome response.

The above hypotheses are not mutually exclusive. Indeed some overlap is logically necessary; in many environments, a homochromic response would have little or no selective value unless the individual also thereafter selected its habitat for background colour.

The first proposition is immediately acceptable: differential predation will always tend to eliminate the less well-matched individuals, regardless of whether the variation among individuals is produced genotypically or phenotypically. Confirmatory data on green and brown *Acrida* (Acr.) and grey and brown *Oedipoda* (Oed.) during predation by chameleons and storks has been obtained by Ergene (1951, 1953c). Grasshopper populations differ from those of many insects in that the second and third propositions can also be demonstrated in a variety of species. The evidence for this is presented below.

While it is usual to suppose that the cryptic coloration which results from homochromic change is the major selective advantage achieved by the mechanism, it is clear that colour change will have other effects. To take an obvious example, dark coloured grasshoppers heat up more swiftly to a higher equilibrium temperature in radiant heat, especially when measurements are conducted on dead, anaesthetized or restrained insects; but freely moving animals, at least under conditions where air temperature as well as radiation is high, show very little difference in body temperature between opposite extremes of coloration (see Uvarov, 1966, pp. 207-224, for a review of the evidence). As it is clear that the blacker animals will always absorb more heat, the behavioural and physiological thermoregulation of individuals of the two extreme colorations must be quite different.

Although a number of earlier observers assumed that the homochromy of grasshoppers on very recently burnt ground was the result of an active colour change, rather than of differential predation, migration or habitat selection (e.g. Poulton, 1926), the first successful experimental work corroborating this was performed by Faure (1932) on *Locusta* and *Locustana* (Oedip.), establishing many of the basic facts, though in qualitative form. Solitary larvae of these species were found to be able to make homochromic responses to white, grey, black, yellow, orange and brown backgrounds, but not to red or pink or green. These homochromic responses were made at the moult following several days' exposure to the

background and only occurred in individuals which were not stimulated by the appropriate factors to be green morphs or to enter gregarious phase (see B and C below). All or part of these results have since been experimentally confirmed in a considerable number of genera by several different authors:

Pyrgomorphidae: *Chrotogonus, Parasphena* (larva only), (Rowell, unpublished).

Eyprepocnemidae: *Tylotropidius* (Burtt, 1961).

Catantopinae: *Melanoplus* (Faure, 1933).

Oedipodinae: *Locusta* Hertz and Imms, 1937; de Wilde and Staal, 1955; Albrecht, 1965; Fuzeau-Braesch, 1966; Nicolas and Fuzeau-Braesch, 1968), *Oedipoda* (Ergene, 1952c *et seq.*; Levita, 1966a), *Oedaleus* (Ergene, 1955b), *Gastrimargus* (Rowell, 1970), *Humbe, Heteropternis* (Rowell, unpublished).

Acridinae: *Acrida* (Ergene, 1950 *et seq.*), *Cannula* (Rowell, unpublished).

Gomphocerinae: *Phorenula* (Burtt, 1951), *Mesopsis* (Rowell, unpublished).

Of the above, only black pigment homochromic change was found in the Gomphocerines, and in *Cannula* and *Tylotropidius.* The orange pigment change appears to be confined to the more geophilous forms, except in the case of *Acrida.* In the Cyrtacanthacridines *Acanthacris* and *Ornithacris* (Rowell, unpublished) no homochromic response has been found, though specifically looked for under experimental conditions.

In a number of these genera, the change to black can take place in the adult, i.e. without a moult, though this requires longer exposure to appropriate conditions (*Phorenula, Tylotropidius,* Burtt, 1951; *Acrida, Oedipoda* and *Oedaleus,* Ergene, 1953b, 1954a; *Locusta,* Albrecht, 1967; Nicolas and Fuzeau-Braesch, 1968). Once made, this change is not reversible, though larvae can assume a pale coloration again following a moult (Burtt, 1951; Ergene, 1953b; Albrecht, 1964; Rowell, 1970). There has been no report of a similar adult change involving the orange pigment.

Subsequent to Faure's work, it has been found that homochromy to blue is impossible, at least among the Oedipodinae. Ergene (1952a, 1955b) has claimed homochromy to green and violet backgrounds in *Oedaleus* and *Acrida,* but this needs substantiation, especially as *Acrida* is sometimes found with purple coloration that appears to be identical with that which is genetically controlled in other species (see Section IIIA). True reds are not matched, but a

close approximation is achieved up to about 600 mμ; in general the range from yellow through orange to red or purplish brown can be matched with great accuracy throughout.

Homochrome adaptation is never total in any large population; even under the most favourable conditions virtually the full range of possible colorations can be found, though the homochrome form greatly predominates and some types, such as completely black animals, are almost never found except on the appropriate background colour (Faure, 1932; Hertz and Imms, 1937; Rowell, 1970). It may be noted that this is also true of those Gomphocerine genera where the polymorphism is probably entirely genetical (see Section III) (Rubtzov, 1935; Peterson and Treherne, 1949; Richards and Waloff, 1954; N. Elsner, personal communication).

2. Light and Mediation

All authors, with the partial exception of Jovančič (1963), agree that the most important environmental factor governing homochromic change is the light to which the insect is subject. Hertz and Imms (1937), Grayson (1942), Levita (1966b), and Rowell (1970) found that homochromy failed in three different Oedipodine genera and *Melanoplus* (Catant.) if kept in the dark. Ergene (1950, 1952b, c, 1953b, 1954a, 1955a, 1956) claimed that larvae and adults of *Acrida, Oedipoda* and *Oedaleus* would make homochromic change even though the eyes were covered with an opaque lacquer; further (1954), that areas of the integument which were similarly lacquered did not make the change while the rest of the exposed insect did. The conclusion drawn was that the epidermal cells are directly responsive to light, and that the eyes do not play an essential role. Levita (1966b), in contrast, found that *Oedipoda* larvae with lacquered eyes made no homochromic response to background at all. Rowell (1970) repeated both of Ergene's experiments with *Gastrimargus.* Lacquered eye animals kept on black backgrounds did show a slight darkening relative to controls on white backgrounds, but no more than a further control group with normal vision which was exposed to black backgrounds for 12 h after each moult. It was concluded that the change seen in the blinded animals was caused by the visual experience during and subsequent to each ecdysis or during temporary damage to the opaque lacquer used, but that this change was slight compared to that seen in normal animals kept continuously on the same dark background. The experiments with

lacquered areas of the cuticle did not confirm Ergene's findings. *Acrida* is a member of a different subfamily and has not been tested for a homochrome reaction by any other worker; but with this caveat, it will be assumed below that the visual response to backgrounds is mediated via the eyes.

Faure and many subsequent workers have found that homochrome change proceeds better under strong illumination than weak. Some claims have been made that homochromy is impossible under weak light, but this is too extreme a view: a significant proportion of *Gastrimargus* larvae made homochromic change to a variety of background colours including both black and orange under maximum illumination of only 23 $\mu W/cm^2$, about one-thousandth of the maximum intensity recorded during control experiments carried out in sunlight. The change took much longer under the weaker light, none being seen before two larval instars had elapsed, but by the final larval instar there was relatively little difference between the two populations (Rowell, 1970).

Hertz and Imms (1937) were the first to point out that the entire range of homochrome coloration in *Locusta* could be described in terms of variation of three components, black, orange, and yellow; this was achieved by comparison of the insect colours with the Ridgeway standards. Levita (1968) has confirmed these results using microspectrophotometric measurements of the reflected light from homochrome adapted *Oedipoda.* Her measurements show that excellent subjective matching can be achieved with backgrounds with dominant reflectivity in the range 574-600 mμ, by altering saturation and lightness in a smaller range of pigments (576-588 mμ). This fits well with the finding (Levita, 1966; Passama-Vuillaume and Levita, 1966) that the epidermal cells of these insects contain orange and yellow granules of tetrapyrrolic character and brown-black granules of ommochrome (see also Section VI).

The orange and yellow mixtures were found by Hertz and Imms to be evoked only on backgrounds which were predominantly of these colours, whereas black pigment was evoked in varying proportion by all backgrounds, being least on white or on yellow-green, and greater on black and far red. Blue background colour elicited grey. From these observations, the authors concluded that the two systems were separately controlled. (In Section VI it is shown that they also use chemically different pigments.) The black pigment was thought to be evoked by the intensity difference between incident and reflected light, and the responses to blue and red backgrounds were taken to

mean that these wavelengths appeared respectively light and dark to the insect eye. Orange pigment was elicited only on backgrounds of that wavelength, and the authors explained its absence in insects raised on white backgrounds in white light by postulating that the short-wave components of less than 550 mμ not only did not elicit but actually inhibited the production of this pigment.

The findings of Hertz and Imms on the control of black pigmentation have been confirmed and extended with *Gastrimargus* (Rowell, 1970), a genus which is very close to *Locusta* but shows little or no phase behaviour. Populations of insects raised in white light on coloured backgrounds were scored for black pigmentation, and the resulting rank order shown to correspond with one exception to the apparent reflectance of the backgrounds, the latter being calculated from the spectral response curves obtained by Bennett *et al.* from *Locusta* retinula cells. The exception was the population reared on orange. The retinula cells are relatively insensitive to light of longer wavelength than 550 mμ, and orange backgrounds would be expected to give marked black pigmentation, as do red. In practice, little black pigment is elicited, and the animals turn orange instead. The most probable explanation for this was thought to be an inhibitory relationship between the two pigment systems, the black and the orange, both of which are evoked under these circumstances. The independence of the black homochrome response with respect to wavelength of light was confirmed by raising groups on white or black backgrounds under a variety of approximately monochromatic lights. In all these experiments, high reflectance backgrounds inhibited the production of black pigment, and absorbant ones facilitated it. The term *albedo response* was suggested for the control of black pigmentation by these factors.

It is not known whether the differential illumination of the retina, which these findings indicate as the trigger stimulus of the albedo response, is topographically fixed, as has been claimed in the isopod *Ligia*. If so, then species with characteristically different positions relative to the horizontal (e.g., grass-living Acridines) would be expected to differ in this topography, or alternatively space-constant visual interneurones (Wiersma and Yamaguchi, 1967) could mediate the response.

Experiments on *Gastrimargus* led to a new hypothesis of the factors influencing the orange pigment system. While orange, brown or yellow backgrounds caused the appropriate homochrome change when illuminated with white light, animals illuminated with

monochrome yellow, red or orange light on white backgrounds made no such change, confirming an earlier result of Grayson (1942) with *Melanoplus.* Backgrounds of other colours under this illumination induced only black pigment response, in proportion to their albedo in the incident light used. The factor present in the first situation which is missing from the second appears to be light of short wavelengths. This is confirmed by the finding that animals simultaneously illuminated with both orange and blue light from discrete sources *do* make a homochromic colour change to orange, though not to either light singly. The response is not affected by reversing the lights, so that the blue source is ventral and the orange dorsal; the response therefore does not depend upon specific areas of the retina, but only demands that some areas receive predominantly short-wave illumination and others, simultaneously, receive predominantly long. This hypothesis is compatible with the results of Hertz and Imms (1937). The electrophysiology of the acridid eye is not so far advanced as to give direct evidence for or against the hypothesis, but the available information is compatible. The retinula cells respond over the range of about 300-600 mμ, and their peak sensitivities form a spectrum so that some are very much more sensitive in the long wavelengths than others (Bennett *et al.,* 1967). Interneurones, which were fed with opposite sign from two such cells of opposite extremes, would effectively function as either long- or short-wave detectors, with little or no response in the green; such units are not yet known from acridid nervous systems but have been described (Swihart, 1969) from lepidopterans. Using elements with these characteristics, a neuronal model can be constructed which will represent the environmental stimuli and the command output to the orange pigment system (Rowell, 1970). The evidence presented in Section VI suggests that this command would ultimately affect the oxidative state of epidermal biliverdin.

It should be stressed that the "orange" pigment system here referred to may not be unitary. But yellow and orange components are present (see discussion above), and though Levita (1968) stresses that these cover only a small range of wavelengths and implies that the distinction may not be real, her published datum points from red-brown insects form a population which differs significantly from those obtained from insects adapted to yellow backgrounds. Subjectively, homochrome insects from these backgrounds appear very different. Retinula cells do not fall into two distinct categories of frequency sensitivities, as would be the minimal requirement to

drive one pigment system in the manner proposed; they form instead a graded population between two extremes, and appropriate combinations of these could give detector systems for several closely spaced wavelengths.

3. Other Environmental Factors

In comparison with other elements of variable coloration, the homochrome responses are relatively unaffected by environmental stimuli other than light.

Temperature is known to influence the development of black pigment in a variety of grasshoppers and locusts, but the relation of this to the albedo response is almost unknown. A number of grasshopper species are generally darker in the colder parts of their range than in the warmer, and in *Chortioicetes* (Oed.) (Key, 1954) this relationship has been experimentally shown to be causal. Grayson (1942) found that low temperatures increased both areas of black pattern and the general level of black pigmentation in *Melonoplus bivattatus* (Catant.) and Okay (1956) found that *Acrida* (Acr.) reared at sublethal cold temperatures (c. 16°C) were darker than normal (32°C) controls, while those reared at high temperatures (40°C+) were much lighter than normal. Duck (1944) had obtained similar variation in both green and brown forms of *Schistocerca obscura* (Cyrt.). rearing them at 21°, 30° and 32°C. Similar effects are known with gregarious phase locusts (see Section IV C.). Nicolas and Fuzeau-Braesch (1968) showed that if gregarious *Locusta* (Oed.) are prevented from developing dark pigmentation by cold treatment, they are thereafter, at normal temperature, rendered able to make a homochrome response to black background, which is normally impossible with individuals of this phase. In *Poekilocerus hieroglyphicus* (Pyrg.) cold temperatures (17° C) caused a retention of melanic pigment in total darkness, which at normal temperatures would have caused it to disappear (Abushama, 1969). This homogeneous body of results apparently shows that the Acrididae differ markedly from the Phasmid *Caransius morosus,* in which melanin and ommochrome formation is inhibited by low temperature (Dustmann, 1964).

Crowding, other than in those species in which it causes phase change or influences the green/brown polymorphism (Sections B and C below) has no apparent effect on homochromic change; humidity, too, affects it only in so far as it biases the green/brown polymorphism. A variety of agents other than temperature are

known to influence black pigmentation, but their effect is probably a general one acting through the responsible endocrine system (see Section V B) and has no special relevance to homochromic change.

4. Interaction of the Homochrome Responses with Other Pigment Systems

The apparent inhibitory relations between the orange and the black pigment systems has been noted above. Both systems are also inhibited to a greater or lesser degree when either green morphs or (in locust species) gregarious forms are produced.

It is usually stated that homochrome responses are absent from green morph grasshoppers. This is not strictly true. In some species the entire body surface is subject to green/brown polymorphism, but in many, especially among the Oedipodinae, there remain some areas of epidermis which retain in a characteristic pattern the brown ground colour, even though the rest of the animal is green. These areas remain capable of giving a homochrome response with either the orange or the black pigment system. However, only very rarely does one see an insect in which it appears that both green and brown pigments are present either in the same or in closely adjacent cells. There is undoubtedly an inhibitory relation between green and black pigmentation. In experiments with *Gastrimargus,* all circumstances which altered the probability of black pigmentation also altered inversely the probability of green; this held to include the case of animals raised on orange backgrounds. As explained above, the orange pigment response which is thus elicited appears to inhibit the black pigment which is expected on the basis of the apparent albedo of orange backgrounds; and these animals were not only less black than expected, but had an unusually high proportion of green morphs (Rowell, 1970). A similar relation between green and black pigmentation was found in *Locusta* by Nicolas (1969), and Nicolas, Cassier, and Fain-Maurel (1969), when the activity of the black system was manipulated with CO_2 concentration. However, the green and black pigment systems are not completely exclusive. Both in the wild and in experimental situations one finds a small proportion of green morph animals with heavy black pigmentation superimposed on the green areas; this is especially frequent in Oedipodine grasshoppers raised on black backgrounds in high humidity (Albrecht, 1967; Rowell, 1970), or captured in corresponding habitats, and is also seen in other groups, e.g., the elongate gramnivorous genus *Mesopsis* (Gomph.) and in

Amphicremna (Acrid.). Nolte (1963) noted that black and green pigments could vary independently in his experiments with *Schistocerca gregaria, Locusta* and *Locustana.*

Homochromic responses were found by Faure (1932) to be absent in *Locusta* and *Locustana* hoppers which were kept crowded and which tended to enter the gregarious phase. This has been confirmed by all subsequent investigation and is now accepted for the locust species (Uvarov, 1966), though crowding does not affect the homochrome responses of related species, such as *Gastrimargus,* which show no locust traits (Rowell, 1970). This is not to deny that the gregarious phase coloration which is found in such locust populations is itself in part influenced by conditions of the physical environment (see Section IV C), but these influences do not result in homochromy. It has recently been shown (Fuzeau-Braesch, 1968; Nicolas, 1969; Nicolas and Fuzeau-Braesch, 1968; Nicolas *et al.,* 1969) that this and several other aspects of the transformation to gregarious phase can be inhibited or reversed by short daily exposures to high concentrations of CO_2. This has itself a small positive effect on black pigmentation (see above), but a much larger one in reducing the number of gregarious phase animals and thus increasing the number of solitarious forms capable of making homochromic responses to black. Only the responses to black backgrounds has been tested in these experiments; whether the orange pigment system is affected in any way is not yet known.

5. Active Selection of Background

In view of the importance of this behaviour for a full explanation of homochromy, remarkably little experimental evidence is available. Ergene (1951a, 1952d, 1953a, 1957) performed a series of experiments using wild-caught *Oedipoda* and *Acrotylus* (Oed.) from a variety of habitats, in which the animals were differently coloured; black grasshoppers from burnt grassland, yellow from clay, grey from chalk, reddish from a terra rosa soil, and speckled yellow from sand. When liberated into a cage containing the different substrates, some 80% of the animals which settled on one of these substrates chose the correct one; similar discrimination was shown by larvae, but it was abolished in all animals when the eyes were lacquered. Experiments performed on *Gastrimargus* adults which had been reared since hatching on white or black backgrounds confirm these experiments, and similar observations have been made in the wild on the same species (Rowell, unpublished observation).

In principle, a preference for a particular background colour could

be built into the animal's genotype. This appears to be the case for other aspects of substrate selection in a wide variety of marine animals, and Meadows (1967) has shown that in the amphipod *Corophium* previous experience of atypical substrates does not alter the preference for typical ones. Such a fixed preference may exist in some acridids, presumably ones with invariant coloration, though none have been specifically identified. It would not, however, suffice for the present examples; all the genera cited above are known to perform homochromic colour change, and the preference for a background colour must therefore be acquired simultaneously with the homochromic coloration. There seem to be three possible ways in which this could be done. In many species, the homochromic coloration extends to the eye, and might be thought to act as a filter over the retinal apparatus. Homochrome backgrounds would therefore tend to be relatively brighter than non-homochrome ones. This seems an improbable explanation, if only because the animal could not discriminate between homochrome and white backgrounds, and the system would clearly not work for black backgrounds. Secondly, the animal can see various parts of its anatomy, and might conceivably match its background with itself by visual comparison. This again seems unlikely; the most affected areas, the dorsal surfaces, are not visible to the animal. The third possibility derives from the fact that appreciable homochromic change requires five or more days' exposure to the background colour. It seems likely that the animals could simultaneously learn this colour, and select it preferentially thereafter, resulting in a sort of visual homeostasis. This hypothesis is supported by an important experiment (Ergene, 1957) in which it was shown that the normal preference of wild-caught grey *Oedipoda* from a grey habitat could be significantly diminished if they were kept for 5-10 days on a black background. A surprising additional result was that the change to the new preference for black was less if the animals were kept in dimmer light inside than if kept in daylight outside; this would have adaptive significance, for the former conditions would produce less pigmentation in the population, but the mechanism by which the effect is achieved is hard to imagine.

B. THE GREEN/BROWN POLYMORPHISM

1. Distribution and Occurrence

A large number of acridid species (and also many other insect groups, including the tettigonioids, mantoids, phasmids, cicadids, and

lepidopterans, to mention some of the best known) have the capacity for a green/brown polymorphism of the pigmentation of the epidermal cells over much or part of the body surface. Closely related to this polymorphism is an associated polymorphism of haemolymph colour; the two share identical or very closely related pigments, and probably functionally linked (see Section VI). Of a sample of East African acridoids, comprising 180 species and 107 genera of the Acridoidea, a green/brown polymorphism was known to occur in 85 and 43 of these respectively (Rowell, unpublished).

The polymorphism may be even more generally distributed than such figures as this suggest. In some species one or the other form is excessively rare; Richards and Waloff (1954) obtained two green forms of *Chorthippus brunneus* (Gomph.), a sample of 2300, and Wise (1966) recorded the fifth known green form of this species from Britain; only two brown forms of the larva of *Acanthacris ruficornis* (Cyrtacanth.) were found in a sample of several thousand wild specimens in Uganda, though the brown form is common under culture conditions (Rowell, 1967); only one green adult of *Catantops kissenjianus* (Catant.), an abundant species, was seen in six years of collecting in Uganda. *Mesopsis laticornis* (Gomph.) was uniformly brown in the Rukwa Valley, Tanzania, in 1956 (Chapman, 1962), but uniformly green in the Murchison Falls National Park, Uganda, in 1967. One, but only one, green adult form has been seen in cultures of *Schistocerca vaga* (Cyrt.) (G. B. Staal, personal communication). Thus in many species one of the colour forms may have been overlooked. This is supported by hormone experiments (see Section V) in which it is possible to obtain morphs unknown in the wild, such as green adult *Acanthacris ruficornis* (Rowell, 1967b), demonstrating that the epidermal cells may retain the capacity for the polymorphism even though the appropriate hormonal climate rarely or never occurs.

It has been frequently reported in those species where both forms are reasonably common that the green form is more abundant in wetter parts of the habitat, or during and after a rainy season (see, e.g., Golding, 1934). As green vegetation is also more probable in the same circumstances, the resultant cryptic coloration is presumed and has occasionally been shown (Ergene, see p. 158) to confer a selective advantage. The correlation of green colour in background and insect does not, however, imply that cryptic coloration is the only aspect of this polymorphism on which selection could act. Albrecht (1964, 1965) has for example shown that the different

morphs in *Locusta* tolerate starvation differently; green forms are more stress-resistant in damp atmospheres, and brown in dry atmospheres (though not so markedly as the *gregaria* form). Similarly, Richards and Waloff (1952) found that population figures for some British Gomphocerines *(Omocestus viridulus, Chorthippus parallelus* and *Stenobothrus lineatus)* suggested a differential longevity correlating with different colour forms, including the green; though it should be borne in mind that the polymorphism of these species is probably largely genetic, and such differences are perhaps more expected in a polygenic situation.

Logically, the same interacting causal hypotheses as shown (p. 157) valid for the homochrome response apply to the green/brown polymorphism. Differential predation has already been acknowledged. There are no data which show that grasshoppers select green or brown environments according to their own morph, but the experiments of Albrecht (above) and others make it probable that they would so select an appropriate humidity; as this is apparently the dominant environmental factor regulating the polymorphism, as shown below, it would probably have the same effect. The issue appears to be less acute than in the homochrome situation, however, as the environment is likely to change more gradually in its overall vegetational state than in the colour of its earths and rocks.

Genetic factors undoubtedly play a part in determining the green/brown polymorphism in many species (see Section III), but most of the experimental evidence concerns the role of environmental factors. As in other aspects of grasshopper coloration, relatively few subfamilies have been investigated, and there seem to be three main groups of experimental animals giving rise to conflicting beliefs, and which may possibly show real differences, at least with regard as to which of the various factors is the most important in determining the polymorphism of the population. These three are the Oedipodinae, the Gomphocerinae, and *Acrida.* The evidence relating to the first two groups is internally consistent, and seems to indicate a predominantly environmentally determined polymorphism in the former (though with genetic modifiers), and a predominantly genetic polymorphism in the latter. Enough data have been obtained for the Oedipodine species to make it sure that genetic variation is of secondary importance. It should, however, be noted that there is a virtual absence of data on the effects of different environments on experimentally maintained populations of Gomphocerines, and the evidence for a predominantly genetic

polymorphism comes either from direct genetic experimentation or by deduction from measurements of wild populations and observation of their stability under varying seasonal conditions. This evidence, while certainly valid, does not exclude environmentally determined phenotypic variation as a further possibility. The only *experimental* evidence against this possibility is that of Rubtzov (1935), who found that in *Chorthippus* and a number of other Gomphocerine genera no experimental manipulation of background, density or humidity ever produced a transition from green to brown or vice versa. Finally, in the case of *Acrida,* there is considerable disagreement between the various workers who have used it.

2. Light and Radiation

It was noted in the previous section that the probability of the green morph is reduced if lighting conditions are such as to favour black pigmentation. Except for this indirect effect, there is no unequivocal link between reflected light and green/brown polymorphism. The green/brown polymorphism of the cyrtacanthacridine genera is not influenced by background colour, and the oedipodine genera are unable to make a homochrome response to green backgrounds, in spite of their ability so to react to albedo and to backgrounds reflecting longer wavelengths. This homochrome response to green has, however, been vigorously claimed for *Acrida bicolor* (Ergene, 1950, 1952a, 1954b, 1955a) and as energetically denied (Jovančič, 1953, 1960, 1963; Okay, 1954, 1956). Okay's experiments were performed in total darkness; many grasshopper species do not eat under these conditions and soon die, but *Acrida* and a few *Locusta* lived and changed from green to brown or vice versa with other experimental factors. *A. turrita* is green/brown polymorphic in E. Africa; a laboratory culture derived from the wild stock remained uniformly green for some generations under conditions of background colour, lighting, humidity and density which would have induced a large proportion of brown forms in cyrtacanthacridine or oedipodine genera (Rowell, unpublished). It therefore seems likely that if these environmental factors are important to *Acrida,* they have thresholds differing from those of the other subfamilies.

It can be speculated why a visual response to environmental colour is apparently suitable to control black and orange pigmentation but not green. One possible reason derives from the mechanism proposed (pp. 162-3 above and more fully in Rowell, 1970) for the colour

discrimination leading to the homochrome responses. The spectral response curves of the different receptors are most different in the long and short ranges, and the comparator cells which are postulated would have difficulty in distinguishing green from yellow. Such a confusion would lead to undesirable interaction of green and orange pigmentation: and in *Gastrimargus* more orange forms than expected are indeed produced on green backgrounds, though these do not affect the proportion of green forms.

The quantity and quality of incident radiation, however, may well play a part in determining the green/brown polymorphism. Jovančič (1963) has suggested that strong *incident* light will tend to produce brown, rather than green forms, with the implication that the latter provides a better shield against excessive radiation. There is no direct evidence that this is the function of the green/brown polymorphism, but a correlation between low light intensities and the green morph has been found in other orthopteroid insects. Willig (1969) found that *Carausius* tended to be green if reared in total darkness, but brown in normal lighting: this was associated with a change in the quantity of biliverdin in the epidermal cells (see Section VI) and was not due merely to masking by other pigments. Passama-Vuillaume (1964, 1965a) has adduced evidence that the labile bile-pigment chromoprotein, which is either solely or partly responsible for the green coloration (see Section VI), is directly affected by incident radiation. In *Mantis religiosa* and *Sphodromantis* it was found that the extracted water-soluble pigment tended to oxidize to brown in far red and infra-red light, and to colourless in blue or ultraviolet light. Normal white light of low intensity left the green pigment unchanged. The same changes were produced in living animals under similar conditions of illumination, and it was suggested that the direct response of the pigment to radiation explained these changes. A similar pigment was found in *Locusta* (Passama-Vuillaume, 1965b), but was much more resistant to colour change under similar conditions of radiation, which was attributed to differences in the bound protein fraction of the pigment. However, the possibility clearly exists that the green pigment of acridids is directly responsive to illumination under some circumstances, and the expected direction of such a response would be that high intensities of white light or of infra-red radiation would favour the brown form. In view of the conflicting reports on *Acrida*, this would be a likely place to look for such an effect.

A correlation of this sort was found by Rowell (1970) in the

oedipodine *Gastrimargus*; otherwise identical cultures illuminated by tungsten light sources produced very significantly fewer green forms when bulbs of higher wattage were used. Air temperature was not appreciably altered by the larger source, and though it is possible that the greater intensity of radiation could produce a higher internal temperature in the insects, this is unlikely in view of the extent to which grasshoppers actively regulate their temperature. A similar effect is suspected in Cyrtacanthacrid larvae. Under culture conditions with tungsten illumination larvae of *Cyrtacanthacris, Acanthacris,* and *Schistocerca vaga* show a pronounced green/brown polymorphism; the population is all green in the first instar, but shows a progressive change to a majority of brown forms in the last larval instar. This effect is accentuated by stronger wattage tungsten bulbs, and by longer illumination cycles, and is inhibited if fluorescent light sources, which are notably deficient in longer wavelengths, are substituted (Rowell, unpublished; W. Loher, personal communication).

3. Humidity

There is general agreement that humidity is the most important single factor in predisposing experimental populations in favour of the green morph (*Locusta* and *Locustana,* Faure, 1932; *Pyrgomorpha cognata* (Pyrg.), Golding, 1934; *Melanoplus sanguinipes* (Catant.), Faure, 1933; *Locusta,* Hertz and Imms, 1937; Albrecht, 1967; *Chortoicetes* (Oed.), Byrne, 1967a, b; *Gastrimargus,* Rowell, 1970; *Acrida,* Okay, 1956; Jovančič, 1953, 1960; *Schistocerca vaga* (Cyrt.), Rowell and Cannis, unpublished; for a dissenting view, see Ergene, loc. cit *supra*). A number of reports linking green forms with fresh as opposed to wilted foodplants (*Schistocerca paranensis, S. gregaria, Gastrimargus africanus,* Hunter-Jones, personal communication and 1962; Hunter-Jones and Ward, 1960; *Locusta* and *Acrida,* Okay, 1953) are probably picking up the same effect.

The ecological and physiological implications of this sensitivity to humidity are of interest. Humid atmospheres will be associated with a larger probability of green backgrounds than will dry ones, but in order that full use may be made of this correlation it would seem necessary to distinguish between (a) the humidity of the microclimate surrounding the insect, which because of its feeding habits and other behaviour will tend to the moist parts of the environment, and (b) the humidity of the atmosphere as a whole, which is more likely to be of significance to the vegetation.

Cutaneous hygroreceptors of grasshoppers (see, e.g., Slifer, 1955; Aziz, 1958; Riegert, 1960) will sample only the former. It has been suggested (Rowell, 1970) that the apparent sensitivity of the green pigment to infra-red radiation may contribute to an assessment of atmospheric humidity, as radiation at the earth's surface varies with this parameter by up to 60% in certain wavelength bands in the far red or near IR (Gates, 1966), changes much greater than those found to influence the green/brown polymorphism under culture conditions. But whatever the possible role of hygrometry by IR detection in the wild, the experimental data indicate pronounced effects of humidity on green/brown polymorphism under conditions where it could play no part, so that some other detector system, presumably neural, must play a major role.

4. Crowding

In locust species, crowded rearing conditions turn experimental populations of larvae into the gregarious phase, which has its own characteristic coloration which excludes both the green/brown polymorphism and the homochrome responses to background colour and albedo. Relatively little work has been carried out on the effects of crowding on the coloration of non-locust species. It is clear that crowding does not invariably influence coloration in grasshopper species, for the normally social species of *Phyteumas* and *Phymateus* (Pyrg.) retain all their normal complex series of coloration changes if isolated experimentally in the first instar (Rowell, 1967a).

In *Gastrimargus* (Oed.) it has been demonstrated that crowding is significant in influencing the green/brown polymorphism in most sex and age categories (Rowell, 1970). The exceptions are that under the experimental conditions used the density effect was overruled by humidity effects in two populations; adult males in high humidity gave only green forms (males have a genetic predisposition to the green form), and female larvae in low humidity produced a uniformly brown population. In the remaining six experimental categories the crowded population had fewer green forms. The nature of the effective stimulus which is derived from other individuals, visual, tactile, or chemical, is not known. It is unlikely that it reflected any profound change in metabolism for there was no difference in the length of the larval development between the crowded and solitary populations, unlike locusts or social pyrgomorphs. The selective advantage of the sensitivity to this factor is also obscure.

In Cyrtacanthacridines the situation is confused. Johnson (1929, 1932) claimed that crowding changed nymphs of *Cyrtacanthacris tartarica* and *Acanthacris ruficornis* from green to brown. This experiment is not fully reported, but it involved the experimental crowding of wild-caught green larvae. Duck (1944) found that solitary larvae of *Schistocerca obscura* (Cyrt.) were green, but when reared two or more to a cage were brown with more or less dense black markings, depending on temperature. The author attributes this to a phase polymorphism, but it is not clear from his description whether the crowded form is analogous to the gregarious phase of *S. gregaria* or the brown forms of *S. vaga, Acanthacris ruficornis* or *Cyrtacanthacris tartarica*; the latter alternative appears more probable. Cultures of these three species develop increasing numbers of brown forms with age, resulting in a majority by the fourth and fifth instar, although in the wild the brown form is very rare (Rowell, unpublished and 1967b). In *S. vaga* crowding increases the probability of brown larval forms in either wet or dry environments by 10% relative to isolated controls, but the effect is less that that due to humidity (Rowell and Cannis, unpublished). Experimental isolation of brown *Acanthacris* did not produce a reversion to green in succeeding instars, but the isolation was not enough to prevent, e.g., pheromonal communication. Some Cyrtacanthacridinae do not respond to culture with a brown form (e.g. *Ornithacris turbida,* Rowell, unpublished) but in many of this subfamily it seems that crowding increases the probability of the brown form.

5. Temperature

Okay (1956), keeping brown *Acrida* (Acr.) larvae in saturated air and total darkness (both being conditions conducive to the green morph), found that at 33°C all larvae eventually became green, whereas as the temperature approached the upper and lower lethal limits at 16° and 46°C the proportion dropped to 50% or less. This result may be interpreted as reflecting more a depression of vitality than a specific effect on the polymorphism. Jovančič (1963 and preceding works) has also consistently stressed the role of temperature in determining the green/brown polymorphism of *Acrida* and of *Mantis.* The evidence is complicated by the apparent need to distinguish between temperature and long-wave radiation (see Section 1 above) and by and large this has not been done. Passama-Vuillaume (1965a) found that the responses to radiation of *Mantis* pigment *in vitro* and in the living animal were constant over

the range 29-30° C: but according to Jovančič (1960) it is only over 30° C that mantises turn brown in response to high temperature. It certainly seems possible that an oxidative change such as Passama-Vuillaume describes could be facilitated by higher temperature. On the other hand, the green forms of *Schistocerca obscura* (Cyt.) remain green with temperatures up to 34° C, but show a progressive lightening of colour from dark green to a pale greenish white, an effect presumably due to inhibition of melanin and black ommochrome (see p. 164); there was no indication of a change to brown (Duck, 1964). In *Carausius* (Phasmidae) the amount of biliverdin in the epidermis is reduced at 28° C, relative to 18° C, and this increases the probability of brown morphs (Willig, 1969).

High temperatures inhibit black pigmentation (both melanin and ommochrome fractions) in both solitary grasshoppers and gregarious phase locusts (pp. 164, 177). In view of the reciprocal relation between black pigmentation and green morph found in the homochrome and other responses of Oedipodines (pp. 165-166) one would expect that under some conditions green pigmentation would be facilitated by high temperatures, not inhibited, but no report of this is available.

C. PHASE COLORATION

The vast literature on phase polymorphism of locusts has been frequently reviewed, two of the most recent and extensive treatments being those of Uvarov (1966) and Albrecht (1967), where further detail and bibliography can be obtained. Here only brief attention will be given to the coloration of the gregarious phase in locust species, and to the interrelation of this and other components of variable coloration.

The characteristic coloration of gregarious locust hoppers is basically a bold alternation of areas of black and yellow or orange; gregarious phase hatchlings are usually black or at least very dark. Such a coloration is well known in, e.g., *Locusta* and *Locustana* (Oed.), and in *Schistocerca gregaria, Nomadacris septemfasciatum,* and *Anacridium aegyptium* (Cyrtacanth.). A similar patterning has also been found in the wild in exceptionally dense populations of grasshoppers which are not normally considered liable to phase change, including *Pyrgodera armata* (Oed.; Popov, 1952), *Faureia milanjica* (Gomph.; Sjöstedt, 1929), and *Chorthippus albomarginatus* (Gomph.; Rubtzov, 1935), though only in *C. albomarginatus* was the

effect reproduced experimentally. In other species of economically important grasshoppers, the high density populations may have colour patterns which differ at least statistically from the normal, and may approach the classic orange and black type, as in, e.g., *Melanoplus sanguinipes* (Catant.) (Faure, 1933; Grayson, 1942) and *Austriocetes* males (Oed.) (Key, 1954). There are also species in which the only correlate of density is a shift in the proportions of the colour variants which occur under all environmental conditions (e.g., *Dociostaurus maroccanus* adults (Gomph.), Uvarov *et al.*, 1951; *Gastrimargus musicus* (Oed.), Common, 1948).

At least three different trends can be discerned in the behaviour of the pigment systems during the assumption of gregarious phase coloration. These are:

(i) increased black pigmentation;
(ii) inhibition of the pigments responsible for both the green and brown ground colours, and thus also of the green/brown polymorphism;
(iii) inhibition of the visually mediated homochrome responses to albedo or to orange backgrounds.

On the evidence of pigment chemistry, it is possible (Section VI) that these trends reflect only two major changes in pigment metabolism. The loss of the green/brown polymorphism and the loss of the orange homochrome response may be two aspects of a single fundamental change in the metabolism of bile pigments; the increase in black pigmentation involves the same metabolic processes as the homochrome response to albedo, and presumably this system is uncoupled from the normal triggering mechanism during gregarious phase.

Most of the literature on the complex of environmental factors that promote gregarious phase deals with phase criteria other than colour (e.g. morphometrics or behaviour). There are some data on the environmental conditions which influence at least the black pigment component. Stimuli derived from crowding appear to facilitate black patterning (as opposed to general melanization) in a variety of grasshoppers as well as the locusts. Instances are recorded for *Anacridium moestum* and *Cyrtacanthacris tartarica* (Cyrt.; Johnson, 1932); *Aiolopus tergestinus* (Oed.; Plotnikov, 1926); *Chorthippus* spp. and other Gomphocerines (Rubtzov, 1935); *Schistocerca obscura* (Cyrt.; Duck, 1944); *Gastrimargus africanus* (Oed.; Rowell, 1970). This response is, however, not entirely general,

for it is lacking in many species closely related to the above (Uvarov, 1966; personal observation). Nolte (1963) claimed a pheromonal effect in *Schistocerca gregaria, Locusta* and *Locustana* facilitating melanization; recent reports of agents with at least some similar properties in *Schistocerca gregaria* and *Chortoicetes terminifera* (Oed.; Anon., 1969) tend to support this suggestion. The non-specific stress effects of crowding, due to constant disturbance, irritation, tactile stimulation, optomotor input, and so on, must not be overlooked, in view of the way in which such input is likely to influence release of corpus cardiacum hormone (see Section V). Rubtzov published as early as 1935 the observation that grasshoppers infested with mites were invariably darker, and assumed that the increased coloration was a result of irritation. Enforced activity and increased CO_2 concentrations both promote black pigmentation of *S. gregaria* hoppers (Husain and Mathur, 1936a, b). Temperature is known to influence the development of black pigment in gregarious *Locusta* and *Schistocerca gregaria* hoppers. High temperatures (c. 40° C) inhibit the pigment and low temperatures (c. 20° C) promote it (Husain and Ahmad, 1936; Stower, 1959; Dudley, 1964; Uvarov, 1966, review; Nicolas and Fuzeau-Braesch, 1968). This seems to be an effect identical with that seen in solitarious locusts and grasshoppers (p. 164), so that is probably not strictly relevant to phase coloration specifically.

The effect of the phase transformation upon the systems responsible for the green/brown polymorphism and for the orange homochrome response is entirely obscure. If all these colours are in fact mainly due to variation of the bile pigment fraction, then it is possible that the various colour states, green, brown, orange and colourless (which last would represent the *gregaria* state), represent different oxidation levels (see Section VI). There are suggestions that some Cyrtacanthacridine larvae may respond to crowding by a switch from the green to the brown morph (see Section IV B), and if this were confirmed, would tend to support the idea that crowding causes a variety of changes in bile-pigment metabolism, and not merely its total absence in the gregarious phase.

V. PHYSIOLOGICAL MECHANISMS

The environmental stimuli reviewed in the preceding section, with the exception of temperature and the possible direct effect of IR radiation on the green pigment, act only on the sensory receptors of

the animal, and are integrated by the central nervous system. (Indeed, control of variable coloration and associated choice of homochrome backgrounds are virtually the only functions which can so far be ascribed to the colour vision of acridoids, which is otherwise certain only from electrophysiology.) All the colour changes are mediated by the epidermal cells. The mechanisms whereby the CNS communicates with the epidermis is the subject of this section.

Of the classical mechanisms whereby such communication is achieved, there is no evidence to suggest a direct nerve supply to the epidermis which could be used for this function. Such innervation has been described from the Hemiptera (Maddrell, 1966); there is no comparable morphological account from the Orthoptera. Neurosecretion, perhaps additionally supplemented by non-neural endocrine organs, appears to be the only alternative, and to date only two of the various pigment changes seem to have any endocrine correlate; more are presumably to be expected.

A. THE GREEN/BROWN POLYMORPHISM AND THE CORPUS ALLATUM

Pfeiffer (1945) showed a correlation between naturally or artificially high titres of corpus allatum secretion and green coloration of the haemolymph in *Melanoplus sanguinipes* (Catant.). This pigment has many resemblances to that found in the epidermis of green morphs, and may be identical (Section VI); it also appears in the haemolymph prior to an epidermal change to green (Ergene, 1954c, and subsequent authors). Joly (1951, 1952) showed that implantation of additional corpora allata into brown individuals of *Locusta* and *Acrida bicolor* increased the number of green morphs in the next instar. This effect has been exhaustively confirmed in *Locusta* (Joly *et al.*, 1956; Joly, 1960; Staal, 1961; Joly, 1962). For effective change to green, the implantation must be made late in the preceding instar, for while earlier implantation produces a variety of effects, such as metathetaley, on the resultant animal in the following instar, it has no effect on coloration in a majority of cases. It was therefore deduced that the pigment system is sensitive to hormone titre only at or immediately around the moult, and that the hormone increase given by the implant is transitory and decreases soon after the implantation. However, Novak and Ellis (1967) found that the sensitive period in gregarious larvae of *S. gregaria* was during

the first third of the instar; whether this reflects differences in animal, phase status or technique is not clear.

Implantation of even a single additional corpus allatum into larvae of *Humbe tenuicornis, Gastrimargus africanus* (Oed.) and *Acanthacris ruficornis* (Cyrt.), species which show the green/brown polymorphism but none of the phase characteristics of the locust species to which they are closely related, induces green forms in subsequent instars. Indeed, several green adult *Acanthacris* developed from implanted larvae, although such a coloration has never been reported in the wild, which demonstrates the continuing competence of the epidermis to respond to the hormonal climate (Rowell, 1967b). The green colour frequently lasted for several stadia, which argues against a merely transitory survival of the implanted organ. It may be that in previous work the large number of implanted glands induced a retrogressive change in those of the host, and thus a long-term reduction in hormone titre. Injection of synthetic juvenile hormone into larvae of *Schistocerca vaga* (Cyrt.) increased the probability of the green morph in subsequent larval instars, while allatectomy resulted in a brown coloration in the next instar, and adultoid coloration and morphogy in the subsequent one (G. B. Staal, personal communication). Allatectomy of green *Syrbilla fuscovittata* (Oed.) induces brown coloration, but neither allatectomy nor implantation affects the green/brown polymorphism of *Gomphocerus rufus* (Gomph.) (W. Loher, personal communication). This not only supports the view that the polymorphism of the Gomphocerinae is genetically rather than environmentally controlled, but also suggests that there may be real differences between the control of the pigment systems of the epidermal cells in this group as compared with Acridines, Oedipodines and Cyrtacanthacridines. There is no information available on the relation between juvenile hormone and the green/brown polymorphism in the Pyrgomorphidae (*Pyrgomorpha* itself well exemplifies this polymorphism) or in the remaining subfamilies.

Cautery of the A and B cells of the pars intercerebralis in *Locusta* led to green larval pigmentation, and other effects associated with hyperactivity of the corpora allata; these persisted if the nervous connections of the corpora allata were destroyed, but not if the corpora themselves were first removed from the animal (Girardie, 1967). The implication of these and similar results is that the A and B cell regions inhibit by their products the secretion of the corpora allata while the C cells facilitate it; this would form a control system

of the green/brown polymorphism which could be readily accessible to neural input from the periphery (Girardie and Joly, 1968).

B. THE BLACK PIGMENT SYSTEM AND THE CORPUS CARDIACUM

The first indication of a humoral factor controlling black pigmentation was obtained by Nickerson (1954, 1956). Injections of haemolymph from gregarious phase *Schistocerca gregaria* hoppers into transiens or solitarious phase recipients resulted in an increase in black pattern; the reverse transfer had no such effects. The active agent was found to be ether-soluble, pH stable, non-proteinaceous and slowly degraded by boiling, which led Nickerson to suggest a sterol; but a peptide could have similar properties and would be a more likely neurosecretory product.

Staal (1961) found that implants of corpora cardiaca into *Locusta* larvae increased their black pigmentation. This was confirmed by Girardie and Cazal (1965), who further showed that ablation of the corpus cardiacum led to transitory loss of pigment. If the pars intercerebralis was also cauterized, cardiectomy resulted in a permanent loss of pigment. Implantation of partes intercerebrales into cardiectomied animals also increased pigmentation; Girardie (1967) showed by microcautery that the active component of the pars is derived from Type C cells. The evidence thus suggests that the black patterning of gregarious larvae is regulated by the secretion of these cells, via the corpus cardiacum, which acts merely as a store. Highnam (1961) and subsequent workers have demonstrated a release of stored neurosecretory material from the corpus cardiacum after a variety of nonspecific stimuli, including flight, presence of mature males, low frequency electric shock, or tumbling in a rotating jar. Tumbling procedures also produced a significant increase in the black pigmentation of *Schistocerca* hoppers (Husain and Mathur, 1936a), and it is probable that action of this sort underlies the darkening properties of such factors as enforced locomotor activity, and crowding (pp. 164-165). Clarke (1966) demonstrated differences in the histological appearance of at least Type A neurosecretory material in the nervi corporis cardiaci I of *Locusta* under different temperature regimes; it will be recalled that this also influences the amount of black pigmentation in *Schistocerca* and *Locusta* larvae (p. 177).

However, the relevance of this system in solitarious locusts or grasshoppers during albedo responses to non-reflectant backgrounds

(Section IV A) is quite unknown. In this response the releasing stimulus is not at all non-specific, but comprises a highly defined optical input. One way in which the gregarious transformation could inhibit the albedo response would be by blocking the pathway from the appropriate visual integration system to the Type C neurosecretory cells, but many other alternative hypotheses are tenable in the present absence of data. There are some complicating data available; Nicolas and Fuzeau-Braesch (1968) confirm that gregarious adult *Locusta* isolated on a dark background will make very little response to the albedo, but if they have been previously raised at high temperatures which inhibit black pigmentation, their response to the dark background approaches that of isolated solitary animals, and they darken very well. This suggests a post-inhibitory excitatory process, though with very long time relations.

C. OTHER ENDOCRINE CORRELATES OF PIGMENTATION

Phase transformation has a number of endocrine correlates, which are discussed in the reviews cited previously. The changes in the black pigment system and in the ground colour associated with phase transformation are described in Section IV C, and the hormonal control of these systems indicated in A and B above could clearly be integrated into the hormonal basis of phase transformation without conceptual difficulty. A number of additional lines of evidence are, however, less easily accommodated. Nickerson (1956) studied the changes in pigmentation which occurred when portions of epidermis from solitarious or gregarious *Schistocerca gregaria* larvae were grafted into hosts of the same or opposite phase status. The results were complicated by degenerative changes, but are none the less suggestive. Grafts into hosts of the same phase produced no changes in either graft or host epidermis until degeneration set in. Solitarious green epidermis grafted into gregarious hosts lost the green colour, as would be expected from the dependence of green colour on high juvenile hormone levels. Grafts of yellow gregarious epidermis into solitarious hosts did not however become green, as might have been anticipated; instead, the yellow colour was maintained, and spread to surrounding host epidermis, in some cases extending over the whole animal uniformly. If these effects were not artifacts of the operational procedure, they may indicate that the response of the epidermis to the determination of gregarious phase is more complex and more persistent than usually thought.

A further interesting but very curious finding is the demonstration by Fuzeau-Braesch (1968), Nicolas (1969), and Nicolas *et al.*, (1969) that short daily anaesthesia with CO_2 reverses or inhibits many of the characteristics of gregarious phase in crowded *Locusta* larvae, including the gregarious coloration and the inability to make a homochrome response to albedo. CO_2 is known to have a variety of effects on neural activity, as seen in its anaesthetic action; the present finding suggests that it may also have specific and long-term effects on neurosecretion, or alternatively on the integrative areas which process gregarizing stimuli.

Ellis and Carlisle (1961) suggested that the prothoracic glands might influence pigmentation in solitarious *Schistocerca* larvae. Removal of about three-quarters of the gland from green fourth instar hoppers caused a change to yellow at the next moult. However, these effects were not found in *Locusta* by Staal. The CO_2 treatment referred to above caused among other effects an unusual degree of retention of apparently functional prothoracic glands in adult *Locusta*, which might support Ellis and Carlisle's contention, but the interactions of the retrocerebral complex and the prothoracic gland are likely to be so complex in the experiments described that it is difficult to draw any useful conclusion from these data. The remaining evidence all suggests that this particular aspect of coloration is primarily a function of corpus allatum activity.

Repeated implantation of supernumary corpora allata into female gregarious *Locusta* resulted in a variety of solitarious characters in the eggs and resultant offspring produced by that female, including pale coloured hatchlings; the dark colour characteristic of gregarious hatchlings was absent (Cassier, 1964). (In *Locustana pardalina* there is the further complication that the phase status of the female determines not only the colour of the hatchlings but also the diapause status of the eggs (Matthee, 1950), which is also a hormonally regulated character.) Together with the evidence cited above, this suggests that the corpus cardiacum and the corpus allatum may act reciprocally in their determination of coloration in solitarious and gregarious coloration, the latter being characterized by low levels of juvenile hormone and high activity of the corpus cardiacum system, resulting in an absence of biliverdin pigments and heavy black patterning, and the solitarious larvae having opposite characteristics. However, this simple apposition of the main endocrine glands is clearly an oversimplification even if coloration alone is considered, and is certainly not a valid general statement of the endocrine basis of phase (see also discussion in Staal, 1961).

The few data on the endocrine correlates of coloration in other orthopteran groups do not illuminate the situation in the Acridoidea. For example, Roussel (1967) and Fuzeau-Braesch (1968) found that alletectomy resulted in black *Gryllus bimaculatus,* while even a fragment of corpus allatum or injection of synthetic juvenile hormone led to orange pigmentation; the effect was thought to be a direct one of hormone on integument. It is difficult to see where this finding relates to the Acridoid data, where melanization and black ommochrome synthesis appears to be effectively independent of corpus allatum function, unless it too indicates an inhibitory interaction between the corpora allata and cardiaca. The differences between the two groups are emphasized by the fact that the coloration induced by higher juvenile hormone levels is characteristic of crickets bred at high density, while in the acridoid locusts the opposite is true.

VI. PIGMENTS

Despite a considerable body of work, the available information on the pigment chemistry of variable coloration is not easy to reconcile, and it is clear that further data are required. Most of the experiments so far have been performed *in vitro* on extracted material; it seems that some of the ambiguities will only be settled by micro-histochemistry which will give information both on the unextracted pigment and also on its distribution in the cells.

There is broad agreement on the range of pigment types found, though it should be noted that the analytic work has been virtually confined to *Schistocerca gregaria* and to *Locusta migratoria* and other Oedipodine species. These pigments are melanins, ommochromes, carotenoids, and bile pigments and other pyrrole derivatives. Other pigments, such as flavins and pterines, are present in minute amounts. The confusion lies in the role that these pigments play in visible coloration. The following points should be borne in mind when assessing the evidence:

i. Some of the pigments belong to chemical families which are still poorly known or have only recently been elucidated, such as the ommochromes.

ii. Pigments exist both in the free form or as the prosthetic group of a chromoprotein. The same prosthetic group can be combined with a range of proteins, and thus acquire different properties, including different colours.

iii. All the important pigments, with the exception of melanin, are

labile compounds which change colour readily with a change in redox potential. Thus biliverdin at different oxidation levels can be colourless, yellow, red or violet, blue or green; and mixtures of these can also give grey, brown, green and orange colours (Lemberg and Legge, 1949). The oxidative state of a pigment extracted into a particular solvent is likely to differ from that of a pigment granule in the cytoplasm, perhaps dramatically.

iv. The colour of light reflected by a pigment depends on its concentration and its dispersal; thus melanin can produce orange, brown or black colour. Finally, pigments are distributed in determined ways in the integument, the epidermal cells, and the haemolymph, and the pigment in lower layers is often masked by those in the upper.

General accounts of pigmentation of acridids or of specific species have been given in recent years by Fuzeau-Braesch (1963, 1965), Nolte (1965), and Uvarov (1966). This account will merely correlate the different views held on the pigmentary basis of variable coloration, and consider the discrepancies between them.

A. THE GREEN COMPONENT OF THE GREEN/BROWN POLYMORPHISM

Views on this pigment have passed through several historical stages. Prior to experimental work it was widely assumed that green pigmentation in phytophagous insects was derived from ingested chlorophyll, a view which became untenable in the late 'twenties. Przibram and Lederer (1933) considered that the green pigment of *Dixippu* haemolymph was derived from a complex of blue and yellow pigments. Further work, reviewed by Goodwin (1952), led to the view that the green pigments of solitary *Locusta* and *Schistocerca* were of this type; the two components were identified as chromoproteins, the blue having as its prosthetic group mesobiliverdin and the yellow having either or both β-carotene or astaxanthine, both carotenoids. This view is accepted by most of the recent reviewers, and supported by recent experimental work on other groups; thus Willig (1969) isolated one biliverdin and four carotenoids, the most prevalent of which was isozeaxanthin derived from β-carotene, from the epidermis of *Carausius*, and four different biliverdins and three carotinoids, principally β-carotene, from *Tettigonia*. In a recent series of papers Passama-Vuillaume (1964, 1965a, b, 1966) and Passama-Vuillaume and Levita (1966) have advanced a different view: that the green pigment is not a complex

of blue and yellow components, but instead is a single water-soluble chromoprotein, having as its prosthetic group IX-α-biliverdin. The studies were initially on mantids, but have been extended to both *Locusta* and *Oedipoda*; slight differences between the Acridoids and Mantoids, as, e.g., in resistance of the pigment to oxidation when irradiated with light, are attributed to differences in the protein fraction.

It is at first sight difficult to reconcile these two views. Many of the biochemical determinations which support the two-pigment hypothesis have been made on haemolymph rather than epidermis (for an acridid example see Dadd, 1961), but this is not the case with the results of Goodwin and Skrisukh (1951) who investigated them separately in both *Locusta* and *Schistocerca.* Further, Blackith and Blackith (1969) found that in Morabine Eumastacids and in *Atractomorpha* (Pyrg.) electrophoresis of haemolymph proteins produce bands which are colourless, yellow, or *green,* not blue. Dadd (1961) and Nayar (1964) have shown that diets deficient in carotene produce blue, rather than green, larvae in *Locusta, Schistocerca* and *Melanoplus* (Catant.), which supports the two-pigment hypothesis. Similar results have been obtained with the lepidopteran caterpillar *Manduca* (Dahlman, 1969) where the pigment is contained in the haemolymph. However, the effects of carotene deprivation were complex, causing the blue biliverdin pigment to be synthesized in all three Acridoid species in circumstances in which it would normally be absent (e.g., in the haemolymph of gregarious locust hoppers) and also disrupting normal melanin and ommochrome pigmentation. The explanation of these effects is not known; no metabolic disorder other than in pigmentation was observed. It is possible that retinene production was sufficiently disrupted to cause malfunction of the visual system, or it is conceivable that the various pigment systems within the epidermal cells are linked by feedback, such that dietary deficiency affects the other pigments merely by removing the normal carotene pigmentation.

It may also be that the discrepancy between the two theories is less than appears. The presence of carotene is not denied by any worker; the argument turns on the colour of the mesobiliverdin-protein complex. It is quite possible that this compound is sufficiently labile to be subject to colour change between green and blue depending on conditions of extraction and analysis. Perhaps both forms exist in the epidermal cells, for there is appreciable variation in the colour of green assumed by a population of green larvae.

B. THE BROWN COMPONENT OF THE GREEN/BROWN POLYMORPHISM, AND THE BLACK AND ORANGE PIGMENT SYSTEMS

The coloration of the brown morph is known (see Section IV) to include components which respond differently under different environmental conditions; thus the Oedipodine genera possess a black pigment system; an "orange" pigment system which produces coloration varying from yellow to reddish or purple-brown, and which may itself be heterogenous; and possibly a separate ground-colour element, which obtains in the absence of any homochromic stimulation of these two systems. There is also the element of pattern, which is dealt with separately below. Unfortunately, few of the chemical investigations have been made on insects whose status with respect to these different components of coloration had been determined. It is perhaps not surprising that a variety of pigments have been implicated in the "brown" coloration. Of the major pigments, melanin is agreed to be confined to the integument; the remaining ommochromes, bile pigments and carotenoids have all been held to be involved in the coloration of the brown morphs.

Redox-sensitive pigments soluble in acidic alcohol can be isolated from all morphs and stages of *Schistocerca,* and of *Locusta* and various other oedipodines, with the exception of extreme green morphs with no areas of brown coloration (Goodwin, 1952). A similar situation pertains in *Mantis* (Susec-Michieli, 1965). Such pigments have been isolated from many other insects. At least part of this fraction consists of ommochrome (phenoxazone) pigments. The simplest of these, xanthommatine, has been isolated by Fuzeau-Braesch (1960, 1968) from *Gryllus* and from *Locusta* and *Oedipoda,* and found identical with the synthesized chemical. There seems little doubt that the black homochrome response to non-reflectant backgrounds is mediated primarily by epidermal ommochrome, together with some cuticular melanin. Ommochrome is present in large amounts in individuals of *Locusta, Gastrimargus* and *Heteropternis* (Oed.) and *Coryphosima* (=*Paracomacris,* Gomph.) which have been experimentally darkened by rearing on a black background, or wild-caught on burnt grassland (Fuzeau-Braesch, 1965, 1966). Melanic patterning of the cuticle overlies more extensive black ommochrome pigmentation of the epidermis in both gregarious and solitarious colorations (Nickerson, 1956; Fuzeau-Braesch, 1965, 1966). This empirical association of the two pigments

may be due to a functional coupling between the synthetic processes which derive melanin from tyrosin and the ommochromes from tryptophane (Fuzeau-Braesch, 1963b). This hypothesis is supported by the finding that mutant albino *Locusta* are devoid not only of melanin but also of xanthommatine in the larval instars (Fuzeau-Braesch, 1968).

The role of ommochrome pigments in other variable components of the coloration is much less certain. Certainly the range of colours which ommochromes are capable of under appropriate redox conditions would provide the entire observed range of "brown" pigments. Goodwin (1952) concluded that they were responsible for the brown ground colour of adult *Schistocerca* and *Locusta* (though not the additional yellow of mature males) and of solitary brown-morph larvae, and this has been followed by several subsequent authors. However, it is not clear that the experimental evidence goes beyond showing that the brown coloration was not due to carotenoids and that ommochromes were present in the animal; in fact, the only analytic data Goodwin presents on the acidic-alcohol-soluble pigments is that they gave rise to pyrrole degradation products, which seems incompatible with ommochromes.

Passama-Vuillaume (loc. cit.) contends that the brown ground colour of *Locusta, Oedipoda,* and *Mantis* is due not to an ommochrome but to the same biliverdin protein complex to which she attributes the green colour, but in a higher oxidative state. Certainly the correlation between the response of the biliverdin compound *in vitro* and of living *Mantis religiosa* to far red and far blue light seems compelling. The red and yellow granules found in epidermal cells of *Oedipoda* which has made a homochromic response to orange or red-brown backgrounds are also considered to be tetrapyrroles derived from biliverdin by oxidation (Passama-Vuillaume and Levita, 1966). This interpretation is in accord with Goodwin's finding of pyrrole products in the acidic-alcohol extract, rather than with his own ommochrome identification; a similar point was made by Okay (1953). However, Passama-Vuillaume's analysis applies to the *water-soluble* brown pigments. Goodwin (1952), Susec-Michieli (1965), and Fuzeau-Braesch (1969) all confirm the presence of ommochromes in brown morphs in considerable amounts, and the former two authors and many previous workers have also found carotenoids. It seems probable that all are involved; it is tempting to suppose that the neutral yellow or yellow-grey

ground colour of brown morph insects which have made no homochromic response (Hertz and Imms, 1937; Levita, 1966; Rowell, 1970) consists of oxidized biliverdin chromoproteins and β-carotene, with ommochromes providing the non-melanic patterning; that the response to low reflectance backgrounds causes synthesis of black ommochrome and some extra melanin; and that orange and red backgrounds result in further oxidation of biliverdin to give pyrrolic pigments of these colours.

A special difficulty is raised by species (e.g., *Gastrimargus* (Oed.), or *Chrotogonus, Parasphena* (Pyrg.)) which become almost pure white when raised on a white background. No analyses have been made of the pigmentation of such individuals, but it seems certain that either they contain an as yet unidentified white pigment masking the remainder, or that they have lost their brown pigments. This last presents no especial problem in the case of the bile pigments, for these can be oxidized to a colourless form; but this is not known to be possible for the carotenoids or the ommochromes, and these would have to be actively removed. As ommochromes are not found in the haemolymph (Goodwin, 1952), this would imply their intracellular breakdown.

C. IMPLICATIONS OF THE ABOVE FOR THE GREEN/BROWN POLYMORPHISM

The attraction of Passama-Vuillaume's interpretation of pigmentation, in which the green and many of the brown colours are derived from basically the same biliverdin pigment, is that it allows the almost ubiquitous green/brown polymorphism to be correlated with a simple redox shift at the cellular level. However, further experimental verification is required before this view can be accepted without reservation. Even if this is the primary mechanism, it still requires to be supplemented by a further command sequence which will inhibit the production of ommochromes in the green morph, and allow their synthesis in the brown morph. Even this does not suffice to explain all observations. For example, while oedipodines are usually either green or "brown" in a given area, which is compatible with the hypothesis, some green individuals are capable of making a homochromic response to a black background without concomitantly losing their green colour (pp. 165-6). It is clear that at least under these circumstances the inhibition of ommochrome synthesis (which appears to be epidermal, Goodwin, 1952) is not complete.

D. PATTERN

Pattern, as used by Fuzeau-Braesch (1965) or Rowell (1970), is a heterogenous category. It includes both exocuticular melanin and epidermal ommochrome. In the case of the black markings which form part of the pattern of, e.g., *Locusta* and *Schistocerca* gregarious larvae there is a close correspondence between the two pigments, as noted in Section II above. However, pattern can also describe variation in colour or density of the epidermal pigments only, as in many larvae of solitarious *Locusta* or of *Gastrimargus.* In these animals the pattern is composed of denser areas of brown or grey pigment, and the moulted exocuticle has no corresponding melanic markings. It is presumed that this pattern is ommochromal, but the remarks in Section B above will show that this does not have to be the case. The melanic pattern of the exocuticle is perhaps the only element of grasshopper coloration in which there seems no remaining ambiquity with regard to the responsible pigments; the detailed confirmation of this has been largely due to Fuzeau-Braesch (1963a, 1965, 1966).

E. THE PHASE COLORATION OF GREGARIOUS LOCUST HOPPERS

In many species gregarious larvae are predominantly black and orange or yellow, in a bold pattern. The black patterning differs from that of the solitary form in amount and distribution, but has the same pigment chemistry. The yellow/orange ground colour is more debatable. Grayson and Tauber (1943) thought that carotene was largely responsible for the differences between solitarious and gregarious coloration of *Melanoplus sanguinipes* (Catant.). Goodwin (1952) concluded that while carotenoids and ommochromes were both present in gregarious *Schistocerca* and *Locusta,* the yellow ground of the former was due solely to carotenoids, while that of *Locusta* in contrast was derived from a partial melanization of the cuticle, and not from underlying pigment. The evidence for this role of carotene in *Schistocerca* is the loss of yellow colour caused by extraction in acetone, although Goodwin's plate and text indicate that only a small fraction of the yellow colour is in fact removed by this treatment. In *Locusta* larvae, acetone treatment produces no obvious change in the whole animal, and it was concluded that the orange colour was due not to carotene, but to some other pigment, probably cuticular melanin. Dadd (1963) raised gregarious

Schistocerca and *Locusta* larvae on diets deficient in carotenoids, and obtained individuals with less than the normal yellow coloration, which supports the view that carotene is the yellow epidermal pigment in *both* species. Histochemistry of frozen sections of epidermis and cuticle is required to elucidate this point.

The evidence seems to suggest that the typical gregarious phase coloration is derived by an overall simplification of the pigment systems in which at least the bile pigment complex is not manufactured. The absence of this pigment, if the appropriate hypotheses as to pigmentation are selected from those reviewed above, could simultaneously explain why gregarious hoppers have a yellow colour, rather than a brown; why they are never green, despite otherwise favourable environmental conditions; and why they are unable to make homochromic response to orange or red backgrounds. Added to this deficiency, gregarious hoppers must be presumed to have modified systems for the synthesis of ommochrome, which produce more black area than in the solitarious forms, but which are less responsive to environmental factors, especially background reflectance.

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