

STUDIES IN INTRASPECIFIC VARIATION

XIV. FIELD OBSERVATIONS ON GREEN-BROWN POLYMORPHISM IN GRASSHOPPERS (ACRIDOIDEA), AND ITS BIOLOGICAL SIGNIFICANCE

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(1) Field data have brought to light the natural occurrence of a type of colour polymorphism, the green-brown polymorphism, in several Acridoidea, in addition to other types which may exist simultaneously. In this type one morph is predominantly green (in some cases blue-grey in adults), and the other predominantly brown (or fawn or buff). (2) It occurs in both adults and older hoppers, and is distinguishable from the Urvovian phase variations and also from the environment-induced colour changes. It is probably genetical in origin. (3) When it occurs simultaneously in a species showing phase variations, it is confined to the phase *solitaria* and does not occur in phase *gregaria*. (4) The proportions of individuals of the two morphs may vary with the species. Either the green or the brown morph may predominate, or the two may occur in equal proportions. (5) The biological significance of this polymorphism is discussed. Its nature is apparently of the "parallel series type", but with more examples it may ultimately prove to be of the "homologous series type" (of Vavilov).

INTRODUCTION

There is occasional mention in the older literature of the occurrence of a type of colour polymorphism in grasshoppers (Orthoptera : Acridoidea) in which 'green' and 'brown' (or buff or fawn) forms occur in the same population (Roonwal, 1945, 1946; Agrawal, 1955; etc.). This polymorphism is to be distinguished from the environment-induced simulation of background colours which have been reported in some grasshoppers (Roonwal, 1937, 1947; Rowell, 1970, 1971; Farrow, 1975), and also from the phase variations of Uvarov

For many years I have accumulated field data on this type of polymorphism in a number of species from South Asia. These data are presented here along with those from a few other species where such polymorphism is known, and the theoretical significance of the phenomenon is discussed. The taxonomic classification followed is that of Dirsh (1961) as modified by Uvarov (1966). This polymorphism occurs in the following species.

Family I. Pyrgomorphidae

1. *Atractomorpha crenulata* (Fabricius)

Family II. **Acrididae**

Subfamily	}	2. <i>Acrida exaltata</i> (Walker)
Acridinae		3. <i>Acrida</i> sp.
Subfamily	}	4. <i>Cyrtacanthacris tatarica</i> (Linnaeus)
Cyrtacanthacridinae		5. <i>Schistocerca gregaria</i> (Forsk.)
Subfamily	}	6. <i>Hieroglyphus nigrorepletus</i> I. Bolivar
Hemiacridinae		7. <i>Gastrinargus africanus</i> (Saussure)
Subfamily	}	8. <i>Locusta migratoria migratorioides</i> (Reiche and Farirmaire)
Oedipodinae		9. <i>Oedaleus abruptus</i> (Thunberg)

RESULTS

Family I. **Pyrgomorphidae**1. ***Atractomorpha crenulata*** (Fabricius)

Material: India: Madhya Pradesh; Sidhi District.

Habitat: Fallow and cultivated fields and grassland; less commonly, sandy-clayey stretches on banks of rivers and water reservoirs.

Colour Morphs

Numerous living examples of adults from Central India showed the occurrence of two main colour morphs, green and brown; occasional clay-coloured morphs were also met with. These morphs are characterised as follows:

Green morph: General colour plain green to green mottled with small dirty white to pale fawn spots all over; the green distributed all over the exposed parts. Eyes with 4-6 olive-green horizontal stripes. Abdomen deep purple dorsally, pale olive-green ventrally. Hindwings purple basally, fading to colourlessness at the margins.

Brown morph: The green of the 'green morph' entirely replaced here by dark fawn to smoky brown; the mottling spots dark smoky. Eye-stripes dark brown. Dorsum of abdomen and wing-base bluish, with occasional purplish tinge; abdominal venter pale brown.

Clay-coloured morph: Is like the brown morph, but with the browns replaced by clay colour in most places; mottling spots dark grey. Dorsum of abdomen and wing-base purple to mauve; abdominal venter clayey, much darker than dorsum.

In adults the green morph was about three times as numerous as the brown (Table I), while the clay coloured morph was uncommon — the proportions roughly were 75: 24: 1. A few intermediates occurred occasionally, but were very rare. The green and brown morphs occurred together in the same field or grassy patch (also vide Roonwal, in press). The clay-coloured morph, however, was found only on dark clayey stretches, as on the banks of streams and small water reservoirs, thus suggesting environmental influence, that is, colour simulation of the background (cf. *Schistocerca gregaria* and *Locusta migratoria migratorioides*).

Agrawal (1955) mentioned only two morphs — green and grey. Apparently, he either did not come across the brown morph, or combined the brown and clay-coloured morphs into a single category. He added that the colour morphs were noticeable even in the hopper stages, but may change from one to the other during the course of post-embryonic development.

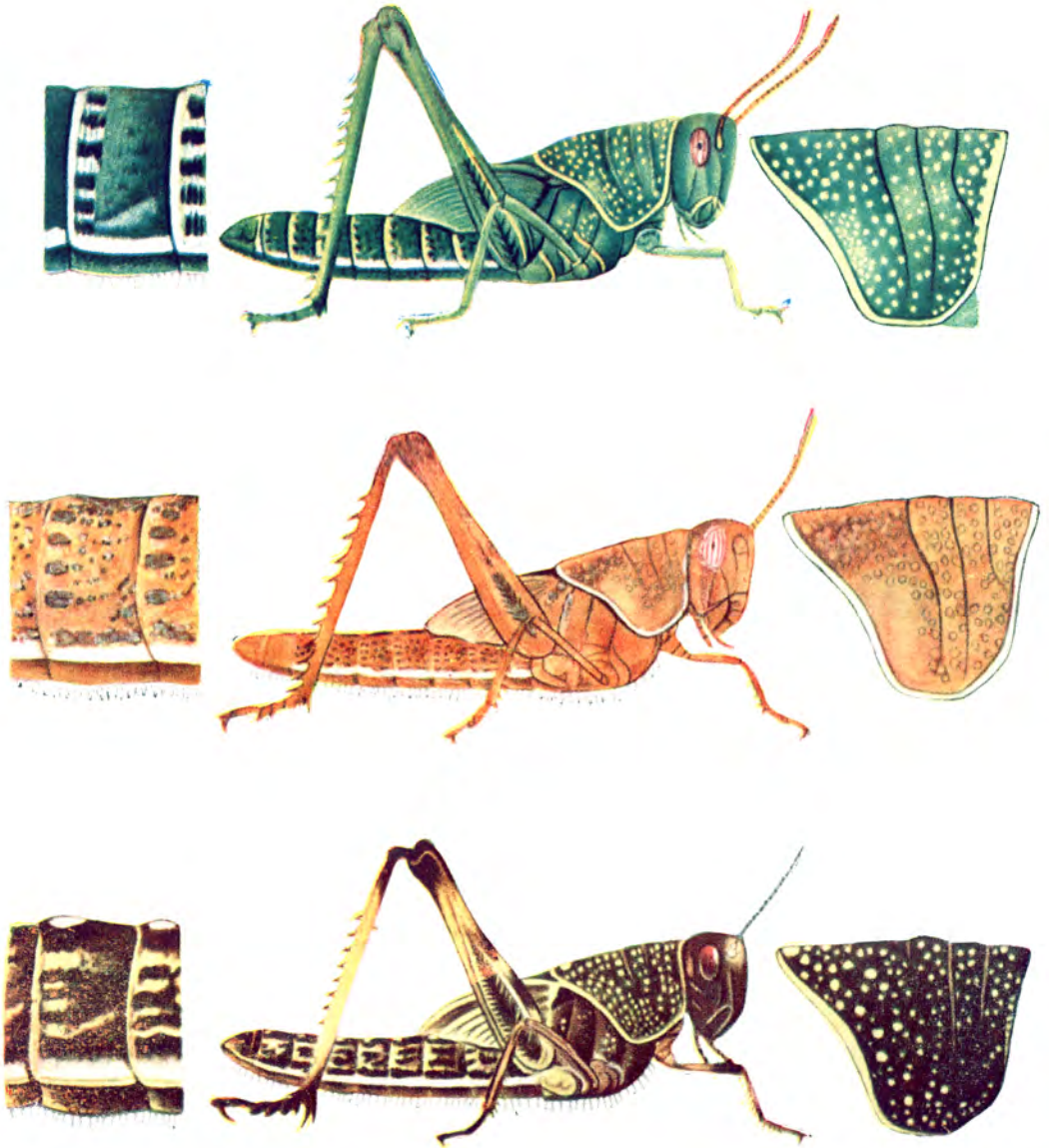


PLATE 1. Fifth stage hoppers of *Schistocerca gregaria*, with pronotum (right) and abdominal (left), enlarged. Upper : Green morph. (phase *solitaria*). Middle : Brown (fawn) morph (phase *solitaria*). Lower : Phase *gregaria*

TABLE I
Proportions of green-brown morphs in some Acridoidea

Species	Proportions in hoppers		Proportions in adults		Remarks
	Green morph	Brown morph	Green morph	Brown morph	
(A) Pyrgomorphidae					
1. <i>Atractomorpha crenulata</i>	Morphs present (proportions not known)		75%	24%	A clay-coloured morph also occurs occasionally (1%), on dark clayey soil.
(B) Acrididae					
2. <i>Acrida exaltata</i>	Condition not known		Morphs present (proportions not known)		
3. <i>Acrida</i> sp.	-do-		-do-		
4. <i>Cyrtacanthacris tatarica</i>	Morphs present (proportions not known)		Condition not known		
5. <i>Schistocerca gregaria</i>	c. 90%	c. 10%	91%	9%	In phase <i>solitaria</i> only
6. <i>Hieroglyphus nigrorepletus</i> (brachypterous form)	4%	96%	8.8%	91.2%	
7. <i>Gastrimargus africanus</i>	Same trend as in adults, but greens rather fewer		65-91%	9-35%	Sexes differ (proportion of greens higher in males)
8. <i>Locusta migratoia migratorioides</i>	Morphs present (proportions vary with season (green morph rising from c. 11% in dry to 63% in wet season))		Same trend as in hoppers (green morph rising from c. 16% to c. 51%)		In phase <i>solitaria</i> only
9. <i>Oedaleus abruptus</i>	Condition not known		Equal	Equal	

Family II. Acrididae

2. *Acrida exaltata* (Walker)

Material: South Asia: India (Madhya Pradesh, Uttar Pradesh, Rajasthan); and coastal Baluchistan (Pasni, etc.).

Habitat: Grassland; and open sandy stretches with low bushes.

Colour Morphs

Numerous examples from Central India and Baluchistan showed the existence of two morphs, the green and the brown, in adults. They are characterised as follows:

Green morph: General colour green all over. A pair of fairly wide, pale brown streaks running horizontally from tip of snout across pronotum and two-thirds of elytra, fading posteriorly into green. A similar but thinner lateral stripe on head running below the larger one. A row of 4-6 cream-coloured linear spots present on the elytra below the brown stripe, and a second brown stripe running below these. Antennae brown with purple tinge. Eyes with 3-10 olive to pale brown stripes. Pronotal keel olive brown. Legs greenish. Abdomen purple green both above and below; sides green. Wings colourless, with a faint yellow tinge; base bluish purple.

Brown morph: Colour pattern as in the green morph, but the green replaced entirely by dark smoky brown; the brown of green morph is here much darker. Eye-stripes greyish chocolate. The purple on lower abdomen almost absent, replaced by pale brown.

3. *Acrida* sp.

Material : India (Jodhpur, Rajasthan).

Is a small, fully-winged species (length with wings:

♂ ♂ 20 mm, ♀ ♀ 25 mm)

Colour Morphs

Both the green and the brown morphs occur commonly in the two sexes.

Green morph : Elytra, head and pronotum deep green; rest of body pale green suffused with brown. Eye-stripes dark chocolate brown, interstripes brown; eyes darker and stripes less clear than in the brown morph.

Brown morph: Body, including elytra, dirty earth-brown. Eye-stripes clearer than in green morph; stripes chocolate, interstripes dirty white.

4. *Cyrtacanthacris tatarica* (Linnaeus)

Material: India.

According to Venkatesh and Harjai (1976, p. 117), after the third instar, both the green and mottled or fawn colour forms appeared in hoppers bred crowded; those reared in isolation remained green throughout the nymphal period. The colour dimorphism was especially marked from the fourth stage onward, but disappeared on eclosion, and all adults were a mottled brown irrespective of the colour pattern of the hopper.

5. *Schistocerca gregaria* (Forsk.)*

Desert Locust (Pl. 1)

Material: South Asia (Baluchistan and western India).

Habitat: Mostly desert areas; in plague years, invading cultivated areas.

Colour Morphs

Two colour morphs, the 'green' and the 'brown', occur in both adults and hoppers (stage III onward) in phase *solitaria* only (not in phase *gregaria*, vide Roonwal, 1945,

* Dirh (1974) regards *S. gregaria* as a subspecies of *S. americana* (Drury).

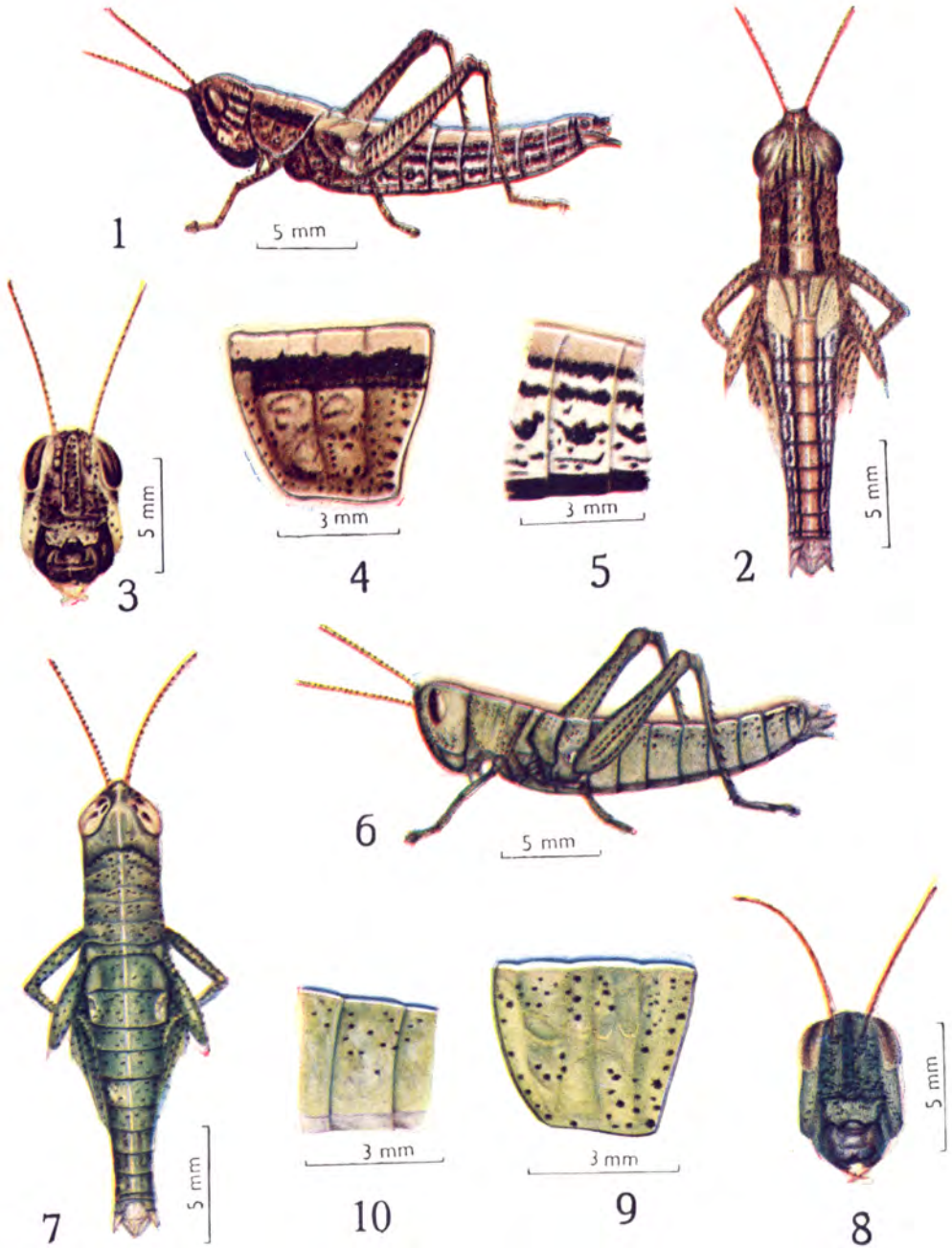


PLATE 2. Hoppers of *Hieroglyphus nigrorepletus* (1-5, stage V, brown morph; 6-10, stage IV, green morph). 1, 6, whole hopper, side view; 2, 7, same, dorsal view; 3, 8, head, front view; 4, 9, pronotum, side view; 5, 10, some abdominal segments, side view.

1946, 1962) in the field as well as in laboratory rearings. They are characterised as follows :

Green morph: Hoppers: General colour green all over; no browns, except for the eye-stripes and antennae. Adults: General colour blue-grey; eye-stripes brown.

Brown morph: Hoppers: General colour fawn all over, some with black pattern, others without it; without a trace of green. Eye-stripes brown. Adults: General colour fawn or buff or blue-grey; eye-stripes brown to chocolate.

The 'green' morph is more common (Table I), about 90% or more (Roonwal, 1945, 1946). Older, phase *solitaria* green hoppers simulate background-colours in experimental boxes painted on the inside (Roonwal, 1937, 1947), but here too fawn hoppers occasionally make their appearance irrespective of the background colour. Roonwal (1946) concluded that the fawn (brown) hoppers and adults are of genetical, and not environmental, origin.

Further, field observations in Western India have confirmed the occasional occurrence of fawn hoppers and adults in small numbers in a population along with green hoppers or blue-grey adults.

6. *Hieroglyphus nigrorepletus* I. Bolivar : Phadkā Grasshopper (Pl. 2)

Material: India: Rajasthan, Uttar Pradesh, Punjab. This species occurs in two forms — a short-winged form (brachypterous) and a fully-winged one (macropterous), the latter being rare; the remarks below apply to the former.

Habitat : Cultivated fields and nearby forest areas

Colour Morphs

Two colour morphs, the green and the brown, occur in adults and older hoppers (stages IV-VI) in the field and in laboratory rearings; the green morphs are less common (Table I), as shown below (cf. *Schistocerca gregaria* above, where the opposite trend occurs):

	<i>Green</i>	<i>Brown</i>
Hoppers (2,152)	4%	96%
Adults (396)	8.8%	91.2%

Both the morphs have a pattern of black dots and streaks, but the general background colour is green in one and brown in the other. The distinction develops from stage IV hopper onward and persists in the adult. In both hoppers and adults, and in both the morphs, females preponderate, but female preponderance is more marked in the green morph (in adults, 85.7%) than in the brown (51.5%) (Also see Roonwal, 1976).

7. *Gastrimargus africanus* (Saussure)

Material : Uganda, Africa (Rowell)

Colour Morphs

Rowell (1967, 1970, 1971), found green-brown polymorphism in all stages after the first instar. Hoppers can be entirely green or brown, with only a few cuticular

melanic markings, or can have an endless variety in between. In wild populations (in atleast the southern, wetter parts of Uganda) the green form predominates and a Iso shows sexual dimorphism in this respect (in an example, green males 91% females 65%), but in laboratory cultures this preponderance of green form is reduced greatly (for example, males 17%, females 4%). Green coloration is favoured by the implantation of corpora allata. Environmental variables affecting green-brown polymorphism are humidity, light and density. The green form is inhibited by crowding, by all factors which promote black pigment, and by lighting conditions with a high proportion of far red and infra-red; it is promoted by high humidity.

8. *Locusta migratoria migratorioides* (Reiche and Fairmaire):

African Migratory Locust

Material: Middle Niger area, West Africa (*Farrow*).

Colour Morphs

Farrow (1975, pp. 65-68 and 83-90) found green-brown polymorphism in both adults and older hoppers (stages III-V) of the solitarious phase.

Green morph: Hoppers: Rather uniform (olive-green to yellow-green); superimposed is a weak pattern of black markings. Adults: Like the hoppers, but the pattern of black (or brown) markings stronger.

Brown morph: Hoppers: Very variable, general colour ranging from "purple through beige and buff to grey and almost black" (p. 68), the last being quite rare; the most common colour was beige. Pattern of black markings as in the green morph. Adults: General pattern pale straw to dark brown, with black markings as in hoppers.

In hoppers the proportion of the green morph is low (11%) in the dry period when the vegetation is withered, and gradually rises (to 63%) in the wet period, with the prevalence of fresh, green grass. The same trend is noticeable in adults (16% rising to 51%) (Table I).

9. *Oedaleus abruptus* (Thunberg)

Material: India: Madhya Pradesh: Districts of Sidhi and Shahdol.

Habitat: Open grassland; also, occasionally, dry leaf litter on forest floor.

Colour Morphs

Numerous examples from Central India showed two colour morphs, the green and the brown; they are characterised as follows:

Green morph: General colour green with some fawn and dark brown areas, thus: antennae, mouth-parts, the first two legs dirty brown; eyes with 4-6 brown vertical stripes and one or two oblique white bands; pronotal keel dark brown. Meso- and metanota and basal two-thirds of abdomen olive-green. Hindlegs and elytra green; wings greenish yellow basally colourless distally, with a broad smoky band in between.

Brown morph: Like the green morph, but with the greens replaced by browns all over except on the wing bases, the meso- and metanota and the basal two-thirds of abdomen which are olive-green.

The two morphs occur in about equal proportions (Table I). They also show some morphometric differences. In females, while the hindfemur length (*F*) shows no difference, both elytron-length (*E*) and the ratio *E/F* are smaller in the brown morph than

in the green one, (the mean value are : *E*, green morph 20.44 mm, brown 19.95 mm; *E/F*, green morph 1.72, brown 1.68). Male samples are too few for comparison of the morphs. In both morphs male lengths are shorter than female, and the ratio *E/F* is lower in males than in females. (Also vide Roonwal, *in press.*)

DISCUSSION

General Trends

Green-brown polymorphism seems to be widespread in grasshoppers (Acridoidea), having been recorded in the families Pyrgomorphidae and Acrididae; in the latter it has been found in four subfamilies. The two morphs may be present in both adults and hoppers. In the latter they generally become differentiated in the older stages (III or IV onward) but sometimes in the earlier ones (after stage I, *Gastrimargus*).

About the proportion of individuals, already three trends are noticeable in adults; the green morph may predominate *Atractomorpha crenulata*, green 75%, brown 24%, clay-coloured 1%; *Schistocerca gregaria*, green 91%, brown 9%; *Gastrimargus africanus*, green 65-91%, brown 9-35%; or the brown may predominate (*Hieroglyphus nigrorepletus*, 8.8 : 91.2); or they may occur in nearly equal proportions (*Oedaleus abruptus*). The proportions may be altered greatly with culture conditions or with the season. In *Gastrimargus africanus* the green morph predominates in the wild state but the proportion is reversed in laboratory cultures. In *Locusta migratoria migratorioides*, proportions vary with the season, the green morph being less common (11-16%) in the dry season, and more common in the wet (51-63%) when fresh, green grass is abundant. When the two morphs are present in a species in both hoppers and adults, the proportions of the morphs in the two developmental stages may show nearly similar trends (*Schistocerca*) or the proportion of green morph may increase with age (*Gastrimargus*).

Sexual dimorphism may also occur. Thus, in *Locusta migratoria migratorioides* there are, on an average, 20% more green females than males while in *Gastrimargus africanus* green males are more common ♂ 91%, ♀ 65%) in the wild state. Where this polymorphism occurs in species showing the Uvarovian phase variations, it is found only in phase *solitaria*, not in phase *gregaria* (*Schistocerca gregaria*, *Locusta migratoria migratorioides*).

Theoretical Considerations

Causal agents

Green-brown polymorphism is to be distinguished from the Uvarovian phase variations, as well as from adaptive simulation of background colours, a phenomenon which is fairly prevalent in the Acridoidea. This distinction was already made in the earlier accounts (Roonwal, 1945, 1946, *Schistocerca gregaria*). It has been re-emphasised recently by Rowell (1970) in *Gastrimargus africanus* and by Farrow (1975) in *Locusta migratoria migratorioides*; here too, as in *S. gregaria*, there are adaptive colour changes for acquiring cryptic coloration. Farrow (p. 66) stated that in hoppers "there were nevertheless two basic colours which were rarely found together in the same individual, namely *green* and *brown*." Adults show the same trend. He further stated that though variations in the proportion of the two morphs in a population may be consi-

dered as an adaptation to the prevailing background coloration in the fledging habitats, this adaptation "is not the primary cause of the variation of green/brown colour morphs" (p. 88).

The character and role of the causal agents have been reviewed by Rowell (1970, 1971). Unlike homeochrome responses to background coloration and environment in general (which effect mainly the brown and black pigment systems of acridids and whose major variation is determined environmentally), green-brown polymorphism has a more complex origin. On the one hand, heredity plays a role, as surmised by the early workers (Roonwal, 1945, 1946, *Schistocerca*), and some workers had even recognised specific genes which alter it (Sansome and La Coeur, 1935, *Chorthippus*; Byrne, 1967a, b, *Chortoicetes*). On the other hand, environment also has an effect which, however, is not well understood. In some species even the most extreme conditions rarely, if ever, induce the production of green or brown morphs. But some environmental (and hormonal) factors readily do so. Thus, in some species green coloration is promoted by corpora allata implantation and by high air humidity, but is inhibited by crowding, by all factors which promote black pigment, and by lighting conditions with a high proportion of far red and infra-red. The responsible pigment has been determined as a protein-linked IX-*a*-biliverdin, which in a higher state of oxidation assumes a brown colour (Passama-Vuillaume, 1966; Passama-Vuillaume & Levita, 1966).

Evolutionary trends

In view of the few known examples scattered over a wide phylogenetic range, the occurrence of green-brown polymorphism may, for the present, be regarded as of the 'parallel type', i.e., evolving independently (polyphletically). It is, however, likely that when more examples are available*, this polymorphism may ultimately prove to be of the 'homologous series type' in the sense of Vavilov (1926, 1928). Vavilov, who discovered this phenomenon in plants, found that these parallel and apparently fortuitous variations often turn out to be regular, widespread and universal. According to him, 'linnaeons' (= species) and genera more or less nearly related to each other are characterised by similar series of variation with such regularity that, knowing a succession of varieties in one genus and linnaeon, one can often forecast the existence of similar forms, and even similar genotypical differences, in other genera and linnaeons; the similarity is the more complete as the linnaeons and genera are more nearly related. Such variations Vavilov called the 'homologous series type.' (For a general discussion of insect polymorphism, vide Dobzhansky, 1951; Ford, 1961; Kennedy, 1961; and Richards, 1961).

When further field work brings to light more examples of green-brown polymorphism, we may be in a better position to decide about its real nature.

* In a sample of East African material, comprising 180 species and 107 genera of Acridoidea, a green-brown polymorphism was found to occur, by Rowell (1971, p. 168) in 85 species and 43 genera, but names were not mentioned.

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