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Natural Selection and the Maintenance of Colour Pattern Polymorphism in the Australian Plague Locust *Chortoicetes terminifera*

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Abstract

Twelve samples of *C. terminifera* from seven locations in eastern Australia were analysed for colour pattern polymorphism. Although there was heterogeneity between the samples the overall frequencies of the colour pattern genotypes were very similar. Males and females showed consistent differences in their genotype frequencies and this is presumed to reflect differential selection between the two sexes. A comparison between observed genotype frequencies and those expected under random mating and in the absence of selection revealed large differences. In particular, genotypes heterozygous for two dominant genes were consistently underrepresented. While these differences could result from non-random mating it is argued that they are more likely to be due to viability differences between the genotypes.

Introduction

The most successful attempts to analyse the action of natural selection in wild populations have come from the study of colour pattern polymorphisms in various groups of animals (Ford 1975). Most colour pattern polymorphisms that have been studied in detail appear to be balanced: that is the selective forces are such that allelic variants are maintained in populations in a state of dynamic equilibrium. While the relevance of such systems to our understanding of the action of selection in general remains unclear (Lewontin 1974) they do provide valuable insights into population processes.

Many species of Orthoptera are known to exhibit colour pattern polymorphisms but only a limited number of studies have been carried out on the genetic basis of this variation (Nabours 1929; Sansome and La Cour 1935; Creighton and Robertson 1941; King and Slifer 1955; Byrne 1967*a*; Dearn 1981; Gill 1981) and few attempts have been made to examine the action of natural selection. A notable exception is the work of Fisher (1939) on colour pattern polymorphism in wild populations of the grouse locust *Paratettix cucullatus* (formerly *P. texanus*) which was one of the first demonstrations of the strength of selective forces in natural populations.

The existence of colour pattern morphs which are common to different but related acridid species (Vorontzovsky 1928) has been taken as evidence that the morphs are genetically determined (Key 1954). This has been confirmed in one system by Byrne (1967*a*) who studied the inheritance of the colour pattern varieties called *albomedia*, *nigrovirgata*, *trilineata* and *rubiginosa* which are seen in the Australian plague locust, *Chortoicetes terminifera* (Walk.) (Key 1954). These varieties are members of a series

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of colour pattern varieties seen in *C. terminifera* and in the eight species of the closely related genus *Austroicetes* (Key 1954). Five of the varieties are identical to those described by Vorontzovsky (1928) in his description of variation in 48 species of acridids and Key retained the original names for the Australian material as well as designating new varieties.

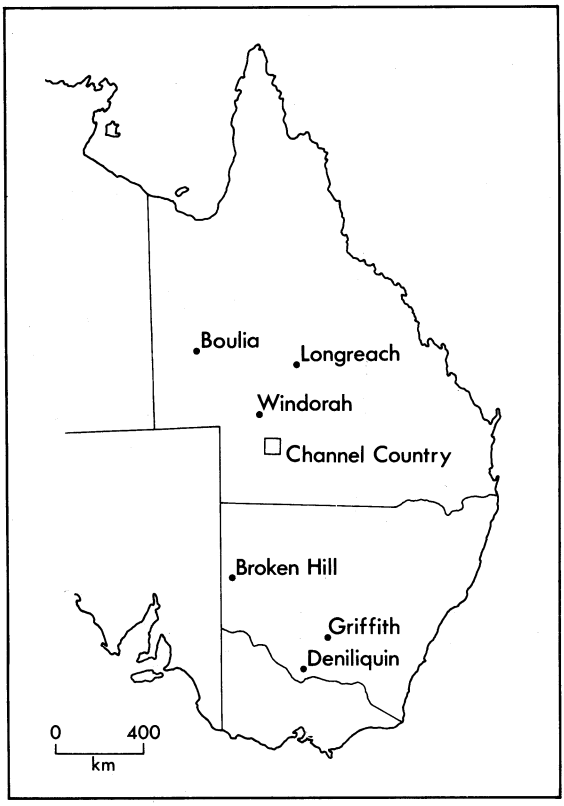

Fig. 1. Map of eastern Australia showing the location of the seven sites.

Byrne (1967*a*) showed that the inheritance of colour pattern variation seen in *C. terminifera* could be explained by the segregation of four alleles (F^a, F^n, F^t, F^r) at an autosomal locus. Of particular importance is the fact that with one exception the heterozygotes are distinguishable both from each other and from the homozygotes on the basis of slight variation of the colour patterns. The system represents, therefore, an excellent opportunity to examine the action of natural selection on a polymorphic locus in natural populations. This paper presents the results of an analysis of colour pattern variation in *C. terminifera* in samples from seven widely distributed locations in eastern Australia.

Materials and Methods

Collections of *C. terminifera* were made from swarms at seven locations (Fig. 1) and are grouped into 12 samples (Table 1), six separate samples being taken from the Longreach area. Details of

the exact location of each sample site are given in an Accessory Publication.* Most samples consisted of material collected using a net mounted on the front of a vehicle. The samples from Longreach E, Channel Country, Windorah and Griffith contain some material caught in light traps. Comparison of the colour pattern morph frequencies in samples caught in light traps and nets from the same site showed no significant difference. The Longreach E sample contained some females caught by hand while they were ovipositing. Material was either scored immediately on collection or preserved by drying for scoring at a later time.

Probability levels associated with statistical tests are expressed using the notation * for $0{\cdot}01 < P \leqslant 0{\cdot}05$; ** for $0{\cdot}001 < P \leqslant 0{\cdot}01$; *** for $P \leqslant 0{\cdot}001$.

Table 1. Collection dates and sample sizes for the 12 samples

Sample	Collection dates	Sex	Sample size	Sample	Collection dates	Sex	Sample size
Longreach A	16.ii.1971	♂	307	Channel Country	22.iii.1972–	♂	370
		♀	337		23.iii.1972	♀	313
Longreach B	24.iii.1971–	♂	470	Broken Hill	25.iii.1972	♂	213
	30.iii.1971	♀	303			♀	150
Longreach C	4.xi.1971	♂	112	Windorah	26.iv.1972–	♂	1048
		♀	87		7.v.1972	♀	856
Longreach D	27.ii.1972	♂	208	Griffith	2.xii.1971–	♂	490
		♀	140		5.xii.1971	♀	155
Longreach E	1.i.1972–	♂	1138	Deniliquin	11.iv.1972	♂	488
	11.i.1972	♀	1387			♀	392
Longreach F	19.ii.1972–	♂	849	Boulia	4.v.1972–	♂	1087
	29.ii.1972	♀	1095		17.v.1972	♀	1428

Results

The Polymorphic System

Byrne (1967*a*) recognized nine distinct phenotypes corresponding to nine of the 10 possible genotypic combinations at the *F* locus, the genotypes F^aF^a and F^aF^r being indistinguishable. It is useful, however, to allocate the nine phenotypes to the four varieties described in Key (1954) (Fig. 2). Key (1954) stated '... many apparent intermediates are found, and there appears to be some degree of variability within the limits of each characteristic pattern...' and it was not until the genetic analysis was carried out that the nature of this variation became apparent.

The F^r allele is the most recessive of the four alleles and the F^rF^r phenotype (*rubiginosa*) is the least conspicuous of the nine colour patterns and appears equivalent to the 'universal recessive' phenotype seen in other polymorphic systems. In this paper, therefore, the F^r allele is referred to as being recessive and the F^a, F^n and F^t alleles as being dominant with respect to this colour pattern polymorphism.

Inspection of the genotypic data in the 12 samples (Table 2) reveals obvious differences between the two sexes in every population. In each case the frequency of *nigrovirgata* is higher in males than females while the frequency of *rubiginosa* is higher in females than males due to differences in the frequencies of the F^nF^n, F^nF^t, F^nF^r and F^rF^r genotypes between the sexes. Analyses of the phenotype number for each population using contingency χ^2 tests (Table 3) show that the differences between

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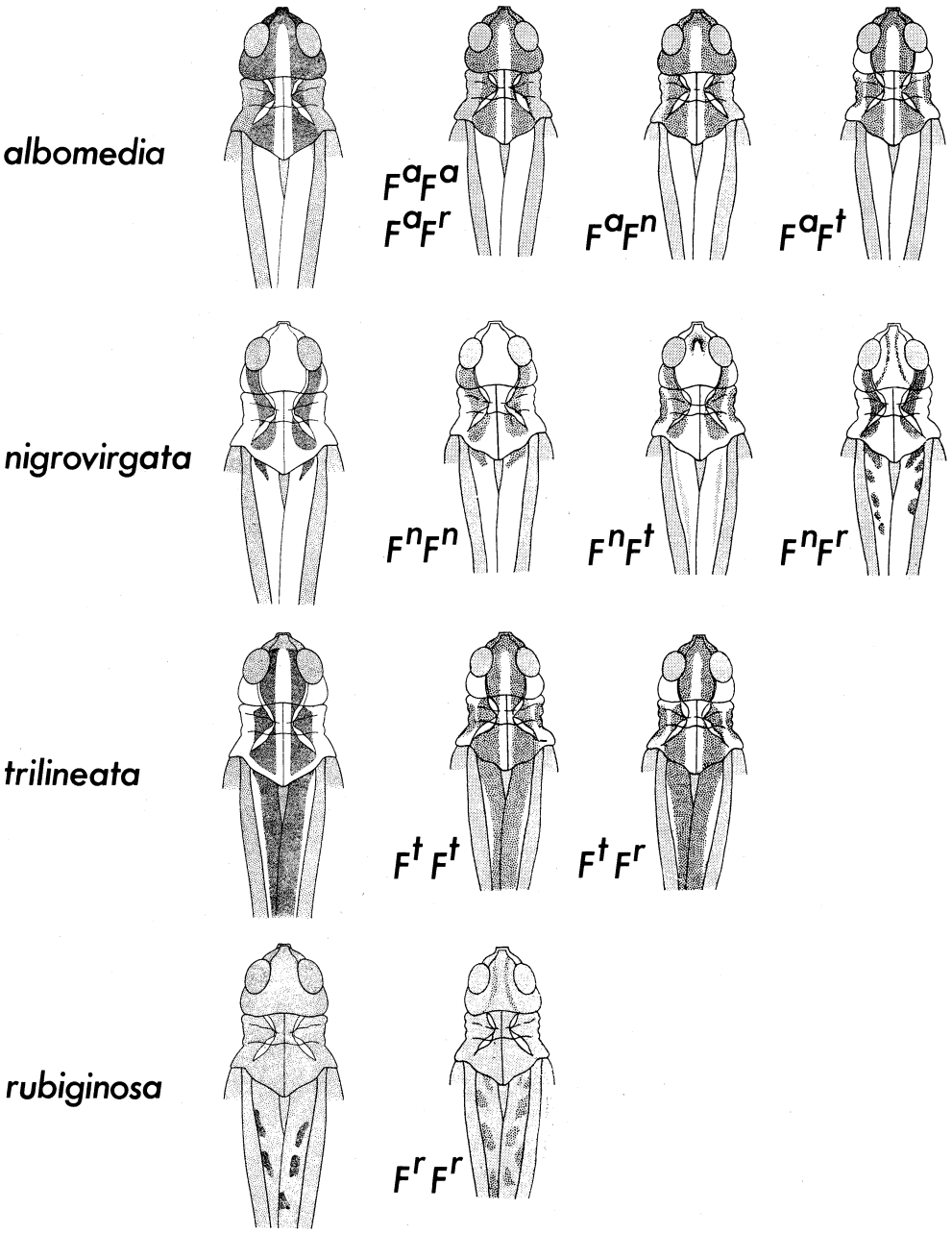

Fig. 2. Drawings of the four colour pattern varieties from Key (1954) together with the phenotypes of the 10 constituent genotypic classes from Byrne (1967*a*).

males and females are significant in all samples except Griffith and the male and female data have, therefore, been analysed separately.

Allele frequencies were calculated for males and females for the 12 samples. It was assumed that all the F^aF^a/F^aF^r individuals were of the genotype F^aF^r since the low frequency of the F^a allele in all samples means that the frequency of F^aF^a individuals is very low. Estimates of preselection genotype frequencies were obtained by calculating the Hardy–Weinberg equilibrium genotype frequencies from the adult gene frequency estimates. χ^2 tests show that the differences between the observed genotype numbers and expected genotype numbers are significant for all 12 samples (Table 4).

Viability Estimates for the Different Genotypes

The ratios between the observed and expected genotype frequencies were used to calculate viability estimates for each genotype in both sexes. These were then standardized across genotypes assigning, as is conventional, the genotype with the highest viability of partial fitness value of 1 (Table 5).

These data show apparent large differences between the viabilities of different genotypes in both males and females. The general agreement between the viability estimates obtained from different samples within either sex lends confidence to the conclusion that the observed viability differences are real. The most obvious feature of these data is that in both sexes individuals heterozygous for two different dominant alleles, i.e. genotypes F^aF^n, F^aF^t and F^nF^t have low relative viability. In both males and females the F^rF^r (*rubiginosa*) genotype has low viability but this is more marked in males.

Geographic Variation

There are a total of six samples from the Longreach area. Field observations on migration and breeding patterns (Davies, unpublished data; D. P. Clarke, unpublished data) showed that the samples termed Longreach A, B, C and D represent respectively generations 1, 2, 4 and 5 in the Longreach area without any detected immigration from other areas. This is confirmed by χ^2 contingency analyses which show that the phenotype frequencies in these four samples are independent of sample in both sexes (males, $\chi^2_9 = 15{\cdot}81$; females, $\chi^2_9 = 2{\cdot}78$). Longreach samples E and F comprise both resident and immigrant individuals because field observations (Davies, unpublished data) showed immigration into the sampled populations of swarming individuals from the Lower Warrego River region to the south-east during the passage of a low pressure trough on 28 and 29 December 1971. χ^2 contingency tests show that the phenotype frequencies are not independent of sample either with each other (males, $\chi^2_3 = 8{\cdot}53^*$; females, $\chi^2_3 = 8{\cdot}71^*$) or with the Longreach A, B, C and D samples (males, $\chi^2_{15} = 32{\cdot}89^{**}$; females, $\chi^2_{15} = 430{\cdot}52^{***}$).

The nine samples comprising Longreach A, B, C and D pooled, Longreach E, Longreach F, Channel Country, Broken Hill, Windorah, Griffith, Deniliquin and Boulia were analysed together and χ^2 contingency tests showed that phenotype frequencies were not independent of sample for either males or females (males, $\chi^2_{24} = 135{\cdot}12^{***}$; females, $\chi^2_{24} = 583{\cdot}33^{***}$).

Table 2. Genotype frequencies in the twelve samples for males and females

Genotype frequencies expected under Hardy–Weinberg equilibrium are given in parenthesis

Sample	Sex	*albomedia*			*nigrovirgata*			*trilineata*		*rubiginosa*
		F^aF^a F^aF^r	F^aF^n	F^aF^t	F^nF^n	F^nF^t	F^nF^r	F^tF^t	F^tF^r	F^rF^r
Longreach A	♂	0·0261	0·0065	0·0000	0·1336	0·0358	0·3616	0·0814	0·2736	0·0814
	♀	0·0119	0·0030	0·0089	0·1068	0·0148	0·2552	0·0623	0·3383	0·1988
		(0·0133)	(0·0080)	(0·0068)	(0·0816)	(0·1391)	(0·2686)	(0·0575)	(0·2188)	(0·2067)
Longreach B	♂	0·0149	0·0064	0·0085	0·0468	0·0638	0·3936	0·0362	0·3851	0·0447
	♀	0·0132	0·0033	0·0066	0·0594	0·0198	0·3300	0·0297	0·3762	0·1617
		(0·0131)	(0·0067)	(0·0065)	(0·0658)	(0·1269)	(0·2495)	(0·0612)	(0·2401)	(0·2302)
Longreach C	♂	0·0089	0·0000	0·0000	0·0982	0·0536	0·2679	0·1964	0·2589	0·1161
	♀	0·0000	0·0000	0·0000	0·0805	0·0460	0·2414	0·1264	0·2414	0·2644
		(0·0023)	(0·0010)	(0·0012)	(0·0580)	(0·1489)	(0·2169)	(0·0953)	(0·2821)	(0·1941)
Longreach D	♂	0·0096	0·0048	0·0048	0·0721	0·0625	0·3702	0·1010	0·3077	0·0673
	♀	0·0071	0·0000	0·0071	0·0643	0·0429	0·3429	0·1071	0·2429	0·1857
		(0·0076)	(0·0046)	(0·0044)	(0·0748)	(0·1480)	(0·2459)	(0·0732)	(0·2434)	(0·1982)
Longreach E	♂	0·0211	0·0018	0·0026	0·1195	0·0527	0·3207	0·1257	0·2856	0·0703
	♀	0·0151	0·0014	0·0079	0·0606	0·0252	0·2999	0·1391	0·3071	0·1435
		(0·0107)	(0·0066)	(0·0075)	(0·0688)	(0·1613)	(0·2256)	(0·0916)	(0·2534)	(0·1746)
Longreach F	♂	0·0082	0·0035	0·0047	0·1366	0·0271	0·3557	0·0742	0·2945	0·0954
	♀	0·0155	0·0055	0·0018	0·0475	0·0137	0·2767	0·0941	0·3689	0·1763
		(0·0091)	(0·0054)	(0·0051)	(0·0644)	(0·1408)	(0·2501)	(0·0679)	(0·2419)	(0·2152)

Channel Country	♂	0·0108	0·0000	0·0000	0·1108	0·0189	0·4108	0·2351	0·1514	0·0622
	♀	0·0319	0·0000	0·0000	0·0671	0·0064	0·3674	0·1981	0·1885	0·1406
		(0·0080)	(0·0060)	(0·0067)	(0·0827)	(0·1776)	(0·2300)	(0·0946)	(0·2422)	(0·1515)
Broken Hill	♂	0·0235	0·0000	0·0141	0·0939	0·0141	0·4178	0·1878	0·2300	0·0188
	♀	0·0200	0·0000	0·0067	0·0667	0·0000	0·3200	0·2667	0·2200	0·1000
		(0·0121)	(0·0084)	(0·0113)	(0·0703)	(0·1896)	(0·1982)	(0·1204)	(0·2551)	(0·1347)
Windorah	♂	0·0134	0·0010	0·0076	0·1317	0·0172	0·3244	0·1050	0·2987	0·1011
	♀	0·0093	0·0000	0·0035	0·0724	0·0140	0·3061	0·1402	0·2617	0·1928
		(0·0081)	(0·0045)	(0·0048)	(0·0704)	(0·1468)	(0·2433)	(0·0746)	(0·2457)	(0·2019)
Griffith	♂	0·0245	0·0000	0·0041	0·1388	0·0265	0·1551	0·2122	0·2980	0·1408
	♀	0·0129	0·0000	0·0000	0·0581	0·0323	0·2258	0·1935	0·3226	0·1548
		(0·0088)	(0·0042)	(0·0077)	(0·0430)	(0·1556)	(0·1710)	(0·1397)	(0·3048)	(0·1653)
Deniliquin	♂	0·0143	0·0000	0·0000	0·1762	0·0102	0·3422	0·0799	0·3545	0·0255
	♀	0·0128	0·0000	0·0051	0·0536	0·0026	0·3571	0·2143	0·2423	0·1122
		(0·0065)	(0·0048)	(0·0047)	(0·0823)	(0·1808)	(0·2357)	(0·0890)	(0·2380)	(0·1582)
Boulia	♂	0·0221	0·0000	0·0028	0·1518	0·0166	0·3045	0·1546	0·2456	0·1021
	♀	0·0147	0·0000	0·0070	0·1106	0·0119	0·2682	0·1148	0·2836	0·1891
		(0·0102)	(0·0065)	(0·0064)	(0·0783)	(0·1551)	(0·2448)	(0·0764)	(0·2389)	(0·1833)

The Green-brown Colour Dimorphism

C. terminifera, like many orthopteran species, exhibits a green-brown colour dimorphism though this is largely limited to females (Key 1954). The proportion of green individuals was scored for all samples except Griffith (Table 6) and three of

Table 3. Contingency χ^2 tests examining the independence of sex and colour pattern phenotype

In the samples Griffith, Longreach C and Longreach D the *albomedia* and *nigrovirgata* classes have been combined because of the low expected numbers of *albomedia* individuals

Sample	d.f.	χ^2	Sample	d.f.	χ^2
Longreach A	3	25·30***	Channel Country	3	17·72***
Longreach B	3	31·82***	Broken Hill	3	15·99**
Longreach C	2	7·30*	Windorah	3	36·99***
Longreach D	2	11·56**	Griffith	2	0·30
Longreach E	3	48·66***	Deniliquin	3	34·45***
Longreach F	3	71·00***	Boulia	3	40·83***

the samples had enough green females to permit an examination of the association between this polymorphism and the colour pattern polymorphism (Table 7). This shows that F^rF^r females have a lower proportion of green individuals than would be expected if there was no association between the two polymorphic systems and confirms the original observations of Key (1954).

Table 4. χ^2 tests comparing observed genotype numbers with genotype numbers expected under the Hardy–Weinberg equilibrium

In most of the comparisons the F^aF^a, F^aF^r, F^aF^n and F^aF^t genotype classes have been pooled to give a total of seven classes and three degrees of freedom. In the samples Longreach C ♂, Longreach C ♀, Longreach D ♂, Longreach D ♀ and Griffith ♀ the F^aF^a, F^aF^r, F^aF^n, F^aF^t and F^nF^n genotype classes have been pooled to give a total of six classes and two degrees of freedom

Sample	Sex	d.f.	χ^2	Sample	Sex	d.f.	χ^2
Longreach A	♂	3	74·37***	Channel Country	♂	3	219·70***
	♀	3	62·72***		♀	3	119·60***
Longreach B	♂	3	172·89***	Broken Hill	♂	3	118·14***
	♀	3	70·04***		♀	3	68·54***
Longreach C	♂	2	27·50***	Windorah	♂	3	283·06***
	♀	2	10·49**		♀	3	168·34***
Longreach D	♂	2	47·03***	Griffith	♂	3	179·50***
	♀	2	18·37***		♀	2	22·20***
Longreach E	♂	3	261·35***	Deniliquin	♂	3	239·46***
	♀	3	252·26***		♀	3	171·81
Longreach F	♂	3	251·84***	Boulia	♂	3	351·66***
	♀	3	226·01***		♀	3	251·02***

Discussion

All the populations analysed in this study were polymorphic with similar frequencies of the colour pattern genotypes across samples. The morph frequencies are similar to those observed in *C. terminifera* by Key (1954) and Byrne (1967*b*) and the same morphs are polymorphic in species of the related genus *Austroicetes*. It would appear,

Table 5. Viability estimates for the nine genotypes

Sample	Genotype								
	F^aF^r	F^aF^n	F^aF^t	F^nF^n	F^nF^t	F^nF^r	F^tF^t	F^tF^r	F^rF^r
				Males					
Longreach A	1·0000	0·4140	0·0000	0·8343	0·1312	0·6860	0·7241	0·6372	0·2007
Longreach B	0·7091	0·5955	0·8153	0·4434	0·3135	0·9836	0·3688	1·0000	0·1211
Longreach C	1·0000	0·0000	0·0000	0·4375	0·0930	0·3192	0·5326	0·2372	0·1546
Longreach D	0·8391	0·6931	0·7246	0·6403	0·2805	1·0000	0·9165	0·8397	0·2256
Longreach E	1·0000	0·1383	0·1758	0·8808	0·1657	0·7208	0·6959	0·5716	0·2042
Longreach F	0·4248	0·3055	0·4345	1·0000	0·0908	0·6705	0·5152	0·5739	0·2090
Channel Country	0·5432	0·0000	0·0000	0·5391	0·0428	0·7187	1·0000	0·2515	0·1652
Broken Hill	0·9213	0·0000	0·5919	0·6336	0·0353	1·0000	0·7399	0·4277	0·0662
Windorah	0·8843	0·1188	0·8464	1·0000	0·0627	0·7127	0·7524	0·6499	0·2677
Griffith	0·8625	0·0000	0·1650	1·0000	0·0528	0·2810	0·4706	0·3029	0·2639
Deniliquin	1·0000	0·0000	0·0000	0·9731	0·0256	0·6599	0·4081	0·6770	0·0646
Boulia	1·0000	0·0000	0·2019	0·8948	0·0494	0·5741	0·9340	0·4745	0·2571
Mean	0·8487	0·1888	0·3296	0·7731	0·1119	0·6939	0·6715	0·5536	0·1833
Standardized mean	1·0000	0·2225	0·3884	0·9109	0·1318	0·8176	0·7912	0·6523	0·2160
				Females					
Longreach A	0·5786	0·2425	0·8465	0·8465	0·0688	0·6145	0·7008	1·0000	0·6220
Longreach B	0·6431	0·3143	0·6481	0·5761	0·0996	0·8441	0·3097	1·0000	0·4483
Longreach C	0·0000	0·0000	0·0000	1·0000	0·2226	0·8019	0·9556	0·6165	0·9815
Longreach D	0·5790	0·0000	1·0000	0·5327	0·1797	0·8642	0·9067	0·6184	0·5806
Longreach E	0·9293	0·1397	0·6936	0·5800	0·1029	0·8753	1·0000	0·7980	0·5412
Longreach F	1·0000	0·5980	0·2072	0·4330	0·0571	0·6496	0·8137	0·8953	0·4809
Channel Country	1·0000	0·0000	0·0000	0·2035	0·0090	0·4006	0·5252	0·1952	0·2328
Broken Hill	0·7462	0·0000	0·2677	0·4283	0·0000	0·7289	1·0000	0·3893	0·3352
Windorah	0·6109	0·0000	0·3880	0·5472	0·0508	0·6694	1·0000	0·5667	0·5081
Griffith	1·0000	0·0000	0·0000	0·9218	0·1416	0·9008	0·9449	0·7220	0·6389
Deniliquin	0·8178	0·0000	0·4506	0·2705	0·0060	0·6292	1·0000	0·4228	0·2945
Boulia	0·9591	0·0000	0·7279	0·9400	0·0510	0·7291	1·0000	0·7900	0·6865
Mean	0·7387	0·1079	0·4358	0·6066	0·0824	0·7256	0·8464	0·6679	0·5292
Standardized mean	0·8728	0·1275	0·5149	0·7167	0·0974	0·8573	1·0000	0·7891	0·6252

therefore, that this polymorphic system is both stable and relatively uniform across different environments.

Key (1954) studied a total of 1169 males and 1443 females sampled from throughout the range of *C. terminifera* (which covers 95% of Australia) and was unable to demonstrate any heterogeneity between samples. By contrast, the present study demonstrated statistical heterogeneity between large samples from seven locations

Table 6. Proportion of green individuals in the 12 samples

Sample	Sex	Proportion green	Sample	Sex	Proportion green
Longreach A	♂	0·0000	Channel Country	♂	0·0027
	♀	0·3798		♀	0·0032
Longreach B	♂	0·0000	Broken Hill	♂	0·0000
	♀	0·2805		♀	0·0067
Longreach C	♂	0·0000	Windorah	♂	0·0000
	♀	0·2874		♀	0·0035
Longreach D	♂	0·0096	Deniliquin	♂	0·0020
	♀	0·0500		♀	0·0995
Longreach E	♂	0·0000	Boulia	♂	0·0018
	♀	0·3079		♀	0·0343
Longreach F	♂	0·0000			
	♀	0·0110			

in eastern Australia. Little can be said about the significance of this heterogeneity, however, in absence of detailed information on migration patterns and the randomness of migration with respect to colour pattern. It is likely that most of the individuals examined in this study were the descendants of individuals breeding originally in south-west Queensland and north-west New South Wales where annual outbreaks occurred between 1969 and 1972 which led to invasions into southern New South

Table 7. Relationship between the colour pattern polymorphism and the green-brown dimorphism

Sample	Green		Non-green		χ_1^2
	F^rF^r	Non-F^rF^r	F^rF^r	Non-F^rF^r	
Longreach A, B, D	9	211	133	427	40·99***
Longreach E	8	419	191	769	78·10***
Boulia	2	47	268	1111	7·27**

Wales and Victoria. The apparent widespread distribution of sample locations in this study may, therefore, be misleading. Differences between the sexes in genotype frequencies are apparent as was observed by Byrne (1967*b*). These could represent a sampling effect due to different habitat associations between the sexes though this is unlikely since the morph frequencies do not differ in samples collected using different techniques. It is assumed, therefore, that they reflect different selection regimes in the two sexes.

The most significant feature of these data is the difference between the observed genotype frequencies and those expected under a random mating, no selection

(Hardy–Weinberg) model. These differences could arise from a number of different causes. First, the low frequency of certain genotypes in the samples could result from a low frequency of matings generating such genotypes. Indeed, it has been suggested that conspicuous colour pattern polymorphisms could evolve in order to distinguish different physiological morphs in that they allow individuals 'genotype to be read at a glance by other individuals' and thus facilitate non-random mating patterns which increase an individuals fitness (Borowsky 1981). However, such non-random mating patterns would only evolve if there already exist fitness differentials associated with the colour pattern morphs. They cannot, therefore, be used as an explanation for the deficiency of certain genotype classes though they could certainly contribute to any such deficits. Nevertheless, it is important that data be collected in natural populations of *C. terminifera* on the pattern of mating with respect to the colour pattern genotype.

A second potential problem in interpreting these data is the possibility of a Wahlund effect due to sample aggregates of populations with different gene frequencies. Unlike the well-known two-allele situation, in the case of multiple alleles the frequency of particular heterozygotes can be either higher or lower and it is not possible to estimate the effect without a knowledge of the covariance matrix of the alleles (Nei 1965; Li 1969). However, the general consistency of the genotype frequencies across the different samples suggests that the deviations from Hardy–Weinberg frequencies are not due to the effects of population subdivision.

The third explanation for the observed deficiency of certain genotype classes is that they result from the action of natural selection. In order to examine this possibility it was assumed that mating was at random with respect to the colour pattern genotypes and that the polymorphic system was in equilibrium. Thus, the before-selection (Hardy–Weinberg) genotype frequencies can be calculated from the after-selection gene frequencies and the ratio of the observed to the expected genotype frequencies will, therefore, represent partial fitness values resulting from a component of egg to adult viability. The problems associated with estimating fitness values from population genotype frequencies are formidable. In particular, fitness values obtained from observed genotype frequencies are necessarily incomplete since they are based on a viability component only and may, therefore, be nullified by other later-acting fitness components (Prout 1969). Nevertheless, deviations from Hardy–Weinberg frequencies can indicate that some form of selection is operating on the genotypes.

The first feature to note with respect to the viability estimates is the magnitude of the differences among the genotypes. These at first appear to be too great to apply to a single polymorphic locus at equilibrium. As previously mentioned, it is possible that these values represent only the relative rankings of the genotype viabilities and the large absolute values could result from a pattern of non-random mating. It must be remembered, however, that balanced polymorphic systems involving 'non-cryptic' characters such as colour pattern variants, unlike polymorphisms for protein sequence variants, are known to involve large selection differentials (Ford 1975).

Although the data have been presented in terms of the single-locus model of Byrne (1967*a*) it appears that the *F* locus is in fact a supergene, a situation well established in other polymorphic systems (Ford 1975). Hawke (1974) observed recombinant progeny in a cross F^aF^t male and F^nF^r female and this was confirmed in further

test matings of the progeny. The *F* locus must, therefore, be regarded as a series of tightly linked genes. Byrne (1967*a*) could not exclude this situation on the basis of the number of progeny he scored and proposed a supergene model involving three loci. In this model the F^rF^r genotype is represented as *ant*/*ant*, F^nF^r represented as *aNt*/*ant* and F^nF^t represented as either *aNt*/*anT* or *aNT*/*ant*, etc. though as discussed later nearly all heterozygotes will be in the repulsion phase.

Association between colour pattern morphs and other phenotypic characteristics have been reported in many grasshopper species. Differences between colour pattern morphs have been observed with respect to tolerance to heat stress (Nankivell 1974), behaviour and morphology (Rubztov 1935), development time (Bradley 1975) and longevity (Richards and Waloff 1954). The observed association between the colour pattern morphs and the green-brown colour dimorphism in *C. terminifera* confirms the previous observations of Key (1954) and Byrne (1967*b*) and shows that the supergene in *C. terminifera* is involved in more than the determination of colour pattern variation.

Green-brown colour variation occurs in many species of acridids (Rowell 1971). In some species the colour variation is under genetic control and is insensitive to the effects of humidity, density or background colour (Rubtzov 1935; Gill 1981). In other species, including *C. terminifera*, which inhabit grasslands exhibiting seasonal changes in moisture content, the green-brown dimorphism is under environmental control by humidity, the moisture content of the diet and, in some species including *C. terminifera*, density (Key 1954; Rowell and Cannis 1971; Otte and Williams 1972). The system determining environmental induction of the colour morphs is itself under genetic control and it is possible to select for sensitivity or insensitivity to environmental induction (Nel 1968). The adaptive value of the dimorphism appears to result from both crypsis and from the fact that the green morph is more stress-resistant at high humidities and the brown morph more-stress resistant at low humidities (Albrecht 1964). It would appear, therefore, that in *C. terminifera* selection acting on the green-brown colour variation will in turn result in fitness differences between the colour pattern genotypes.

The second feature of the viability estimates is that the genotypes with the lowest viabilities are those genotypes that are heterozygous for two dominant alleles. In terms of the supergene model this means that in natural populations chromosomes containing dominant alleles in coupling must be very rare. Individuals with phenotypes corresponding to genotypes with three dominant alleles have been observed in the field and laboratory (Hawke 1974) so that one must presume they are normally eliminated by selection. It appears, therefore, that the components of the supergene exhibit extreme linkage disequilibrium with four of the possible chromosomes (*ANt*, *aNT*, *AnT* and *ANT*) at an extremely low frequency and not recorded in this study. The low viability of genotypes with two different dominant alleles would provide a rationale for the existence of the supergene complex through the modification of linkage relationships under natural selection (Fisher 1930; Mather 1943; Bodmer and Parsons 1962).

The reality of the viability measures gains support from the fact that the situation in *C. terminifera* is remarkably similar to that observed in the grouse locust *Paratettix cucullatus* by Fisher (1939). Colour pattern variation in *P. cucullatus* is controlled by 25 genes. 24 of these genes form a supergene and of these 23 are dominant and one is recessive (Nabours 1929). Fisher showed in an analysis of samples from

six natural populations that, within the supergene, heterozygotes for two dominant genes had their viability reduced by at least 40%. The same observation in an entirely different polymorphic system suggests a phenomenon of considerable interest.

Fisher (1939) pointed out that the low viability of double dominant genotypes was not observed in his analysis of Nabour's laboratory breeding experiments on a related species *Apotettetix eurycephalus*. Similarly, Byrne (1967*a*) in his study of the inheritance of the colour patterns in *C. terminifera* did not observe any significant deviations from Mendelian proportions in the progeny of different crosses. Fisher concluded that 'The cause of elimination is thus probably not a lack of physiological viability ... but some cause such as elimination by predators, which is inoperative in conditions of culture.' While predators may play some role in determining the low viability of the double dominant genotypes in natural populations one would not expect this effect to be observed in all samples. It may be significant that the two natural populations at Coonamble, N.S.W., analysed by Byrne (1967*b*), showed no evidence of the low viability of double dominant genotypes. These populations appeared to be at low density in contrast to the high density swarming populations analysed in this study and there is evidence that selection coefficients are effected by the degree of crowding experienced by the individuals (da Cunha 1949; Birch 1955; Lewontin 1955; Battaglia 1958; Sokal and Karten 1964). Thus it is possible that the low viability of the double dominant genotypes is only manifested under crowded conditions.

If the viability values for the double dominant genotypes in *C. terminifera* are real then they would impose restrictions on the frequencies of the three dominant genes (F^a, F^n and F^t) since increasing frequencies of these genes would result in an increasing genetic load. This effect could account for the high frequency of the recessive allele (F^r) in all populations. The proposed viability structure does not, however, explain the persistence of the three dominant genes in all populations. Each dominant gene might indeed exhibit heterozygote advantage with the recessive allele as proposed by Fisher (1939) for *P. cucullatus*. The F^rF^r genotype does appear to exhibit low viability in all samples but there is no evidence from the viability estimates of heterozygote advantage. The continued maintenance of the three dominant genes in stable equilibrium frequencies in a situation where they exhibit reduced viability when in combination would imply a complex selection regime. Certainly the different selection regime in the two sexes could be an important factor (Mandel 1971; Kidwell *et al.* 1977) as would be a pattern of non-random mating. *C. terminifera* being a locust, is subject to large fluctuations in population density (Casimir 1962; Magor 1970; Clark 1972; Farrow 1977) and these will be accompanied by changes in the frequencies of the green-brown morphs which will in turn exert selection pressures on the colour pattern genotypes. It would be naive to expect a single explanation for the polymorphism as the extensive work on the colour pattern polymorphism in the land snail *Cepaea nemoralis* has shown (Jones *et al.* 1977). Future work will require a detailed study of the ecology of the different genotypes under a variety of environmental conditions.

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References

Albrecht, F. O. (1964). État hygrometrique, coloration et resistance chez l'imago de *Locusta migratoria migratorioides* (R. et. F.). *Experientia* **20**, 97–8.

Battaglia, B. (1958). Balanced polymorphism in *Tisbe reticulata*, a marine copepod. *Evolution* **12**, 358–64.

Birch, L. C. (1955). Selection in *Drosophila pseudoobscura* in relation to crowding. *Evolution* **9**, 389–99.

Bodmer, W. F., and Parsons, P. A. (1962). Linkage and recombination in evolution. *Advan. Gen.* **11**, 1–100.

Borowsky, R. (1981). Tailspots of *Xiphophorus* and the evolution of conspicuous polymorphism. *Evolution* **35**, 345–58.

Bradley, J. S. (1975). Population dynamics and natural selection in a mixed colony of grasshoppers. Ph.D. Thesis, University of Liverpool.

Byrne, O. R. (1967*a*). Polymorphism in the Australian Acrididae I. Inheritance of colour patterns in the plague locust, *Chortoicetes terminifera*. *Heredity* **22**, 561–8.

Byrne, O. R. (1967*b*). Polymorphism in the Australian Acrididae. II. Changes in colour pattern gene frequencies in the plague locust, *Chortoicetes terminifera*. *Heredity* **22**, 569–89.

Casimir, M. (1962). History of outbreaks of the Australian plague locust, *Chortoicetes terminifera* (Walk.), between 1933 and 1959 and analysis of the influence of rainfall on these outbreaks. *Aust. J. Agric. Res.* **13**, 674–700.

Clark, D. P. (1972). The plague dynamics of the Australian plague locust *Chortoicetes terminifera* (Walk.). In 'Proceedings of the International Study Conference on the Current and Future Problems of Acridology, London 1970'. (Eds C. F. Hemming and L. H. C. Taylor.) pp. 275–87. (Centre for Overseas Pest Research: London.)

Creighton, M., and Robertson, W. R. B. (1941). Genetic studies on *Chorthippus longicornis*. *J. Hered.* **32**, 339–41.

Cunha, A. B. da (1949). Genetic analysis of the polymorphism of colour pattern in *Drosophila polymorpha*. *Evolution* **3**, 239–51.

Dearn, J. M. (1981). Latitudinal cline in a colour pattern polymorphism in the Australian grasshopper *Phaulacridium vittatum*. *Heredity* **47**, 111–19.

Farrow, R. A. (1977). Origin and decline of the 1973 plague locust outbreak in central western New South Wales. *Aust. J. Zool.* **25**, 455–89.

Fisher, R. A. (1930). 'The Genetical Theory of Natural Selection.' (Clarendon Press: Oxford.)

Fisher, R. A. (1939). Selective forces in wild populations of *Paratettix texanus*. *Ann. Eugen.* **9**, 109–22.

Ford, E. B. (1975). 'Ecological Genetics.' (Chapman and Hall: London.)

Gill, P. (1981). The genetics of colour-patterns in the grasshopper *Chorthippus brunneus*. *Biol. J. Linn. Soc.* **16**, 243–59.

Hawke, A. D. (1974). Genetic studies of polymorphism in laboratory and natural populations of the Australian plague locust, *Chortoicetes terminifera*. Ph.D. Thesis, Australian National University, Canberra.

Isley, F. B. (1938). Survival value of Acridian protective coloration. *Ecology* **19**, 370–89.

Jones, J. S., Leith, B. M., and Rawlings, P. (1977). Polymorphisms in *Cepaea*: a problem with too many solutions? *Ann. Rev. Ecol. Syst.* **8**, 109–43.

Key, K. H. L. (1954). 'The Taxonomy, Phases, and Distribution of the Genera *Chortoicetes* Brunn. and *Austroicetes* Uv. (Orthoptera : Acrididae).' (CSIRO: Canberra.)

Kidwell, J. F., Clegg, M. T., Stewart, F. M., and Prout, T. (1977). Regions of stable equilibria for models of differential selection in the two sexes under random mating. *Genetics* **85**, 171–83.

King, R. L., and Slifer, E. H. (1955). The inheritance of red and blue hind tibiae in the lesser migratory grasshopper, *Melanoplus mexicanus mexicanus* (Saussure). *J. Hered.* **46**, 302–4.

Lewontin, R. C. (1955). The effects of population density and composition on viability in *Drosophila melanogaster*. *Evolution* **9**, 27–41.

Lewontin, R. C. (1974). 'The Genetic Basis of Evolutionary Change.' (Columbia University Press: New York.)

Li, C. C. (1969). Population subdivision with respect to multiple alleles. *Ann. Hum. Genet.* **33**, 23–29.

Magor, J. I. (1970). Outbreaks of the Australian plague locust (*Chortoicetes terminifera* Walk.) in New South Wales during the period 1937–1962, particularly in relation to rainfall. Anti-Locust Mem. No. 11.

Mandel, S. P. H. (1971). Owen's model of a genetical system with differential viability between sexes. *Heredity* **26**, 49–63.

Mather, K. (1943). Polygenic inheritance and natural selection. *Biol. Rev.* **18**, 32–64.

Nabours, R. K. (1929). The genetics of the Tettigidae (grouse locusts). *Bibl. Genet.* **5**, 27–104.

Nankivell, R. N. (1974). Interactions between inversion polymorphisms and the colour pattern polymorphism in the grasshopper *Austroicetes interioris* (White and Key). *Acrida* **3**, 93–111.

Nei, M. (1965). Variation and covariation of gene frequencies in subdivided populations. *Evolution* **19**, 256–8.

Nel, M. D. (1968). Selection at high humidity for green and brown *solitaria* hopper coloration in *Locustana pardalina* (Walker). *S. Afr. J. Agric. Sci.* **11**, 163–72.

Otte, D., and Williams, K. (1972). Environmentally induced color dimorphisms in grasshoppers. *Syrbula admirabilis. Dichromorpha viridis*, and *Chortophaga viridifasciata*. *Ann. Ent. Soc. Am.* **65**, 1154–61.

Prout, T. (1969). The estimation of fitnesses from population data. *Genetics* **63**, 949–67.

Richards, O. W., and Waloff, N. (1954). Studies on the biology and population dynamics of British grasshoppers. Anti-Locust Bull. No. 17.

Rowell, C. H. F. (1971). The variable coloration of the acridoid grasshoppers. *Adv. Insect. Physiol.* **8**, 145–98.

Rowell, C. H. F., and Cannis, R. L. (1971). Environmental factors affecting the green/brown polymorphisms in the cyrtacanthacridine grasshopper *Schistocerca vaga* (Scudder). *Acrida* **1**, 69–77.

Rubtzov, I. A. (1935). Phase variation in non-swarming grasshoppers. *Bull. Ent. Res.* **26**, 499–524.

Sansome, F. W., and La Cour, L. (1935). The genetics of grasshoppers: *Chorthippus parallelus*. *J. Genet.* **30**, 415–22.

Sokal, R. R., and Karten, I. (1964). Competition among genotypes in *Tribolium castaneum* at varying densities and gene frequencies (the black locust). *Genetics* **49**, 195–211.

Vorontzovsky, P. A. (1928). On the question of homologous series of colour variation in Acrididae. (In Russian.) *Bull. Orenburg Plant Prot. Sta.* **1**, 27–39.

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