VARIATION OF CHIASMA FREQUENCY IN AND BETWEEN
NATURAL POPULATIONS OF ACRIDIDAE

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1. INTRODUCTION

Given any significant heterozygosity the genetic stability and variability of populations must be affected by any variation of chiasma frequency that may occur (Darlington, 1939; Mather, 1943; Thoday, 1953). Natural populations of grasshoppers (*Myrmeleotettix maculatus* (Th.) and *Chorthippus parallelus* (Zett.)) have therefore been examined by analysis of metaphase chiasma frequencies in males to see whether such variation is to be found.

2. MATERIAL

The populations sampled were in the north and south of England (the Sheffield region, and the Ascot and New Forest regions respectively). The grasshoppers were collected in the early evening and their testes fixed within two hours of collection in Strong Flemming's solution. The sections were stained with crystal violet. Chiasmata were counted in five cells per individual and usually in eight individuals per sample.

3. RESULTS

(i) *Chiasma frequencies*

Though the experimental results are limited they seem to demonstrate that variation of chiasma frequency does occur in and between these natural populations. In both *Myrmeleotettix* and *Chorthippus* it was found (i) that there were significant differences between individuals within populations (compare Elliott, 1954), and (ii) samples from different areas had significantly different chiasma frequencies.

In *Myrmeleotettix* the two high altitude (over 1,000 feet) northern populations had lower chiasma frequencies (mean = 14.36) than the two southern populations which were at low altitudes (mean = 15.18). An analysis of the relevant data is given in table 1. These differences in chiasma frequency between areas might be related to climate: the high altitude northern populations were found in cooler, wetter areas than the southern populations.

Samples of *Myrmeleotettix* were also obtained from three medium and low altitude northern populations and their chiasma frequencies varied between those characteristic of the high altitude northern and those characteristic of the southern populations.

All the populations of *Chorthippus* were at low altitudes. Data were obtained from one northern population (two samples) and two southern populations (Ascot and New Forest). The samples from the north (mean = 14.54) had a significantly lower chiasma frequency ($P < 0.01$) than those from the south (mean = 15.51).

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It seems unlikely that the differences of chiasma frequency are directly caused by summer environmental differences for the following reasons :—
 (a) One population of *Chorthippus* was sampled both at mid-day and in the early evening. The two samples had similar chiasma frequencies. (b) Five populations (four *Myrmeleotettix* and one *Chorthippus*) were each sampled in

TABLE 1

Analysis of variance of number of chiasmata in the Myrmeleotettix field samples from the high altitude northern and low altitude southern populations (means listed in table 2)

Source	n	Mean square	P
Areas	1	52.8125	<0.01 †
Years	1	4.05	...
Years × areas	1	2.45	...
Between populations within areas	2	1.325	...
Residual interaction	1	3.725	...
Total between samples	6	10.9479	about 0.05 †
Between individuals within samples (error 2)	48	4.6880	<0.001 *
Total between individuals	54	5.3836	<0.001 *
Within individuals (error 1)	224	1.1268	...

* Compared with error 1.

† Compared with error 2.

TABLE 2

Chiasma frequencies in some of the Myrmeleotettix samples

			Field samples				
			New Forest		High altitude North		
			1955	1956	1955	1956	
Population 1	.	.	.	15.58	15.00	14.58	14.28
Population 2	.	.	.	...	14.95	14.20	14.40

	Greenhouse experiments (1956)					
	New Forest			High altitude North		
	Experiments			Experiments		
	1	2	3	1	2	3
	Population 1	...	15.38	15.13	...	...
Population 2	...	...	...	14.50	14.43	14.13
Population 3	15.38	...	...	...	...	...

different months of the same summer. There was no significant difference between the samples collected earlier and those collected later in the summer. (c) Four populations were sampled in both 1955 and 1956 and there was no significant difference between years, though the summer of 1955 was hot and dry and that of 1956 very cold and wet. (d) Three experiments were carried out, two starting with adults and one with fourth instars, to test whether the differences of chiasma frequency between populations of *Myrmeleotettix* would still be evident if individuals from different populations were kept together in the same environment (a greenhouse in Sheffield) for a few days prior to the time when the chiasmata were actually formed. Analysis of variance showed that the difference between the high altitude and the southern populations was not affected and there was no significant difference between field and greenhouse samples. Table 2 summarises the data.

All these five tests suggest that the differences in chiasma frequency between areas are fairly stable. It seems reasonable to conclude that the southern populations of *Myrmeleotettix* and *Chorthippus* have a consistently higher chiasma frequency (and hence more genetic recombination) than certain of the northern populations.

(ii) Supernumeraries

Supernumerary chromosomes were found in some individuals in five out of the eight populations of *Myrmeleotettix* studied. Individuals with supernumeraries usually had one or two per cell and these chromosomes were never found paired with members of the "normal" complement at first meiotic metaphase (fig. 1).

FIG. 1.—1st meiotic metaphase. *Myrmeleotettix maculatus*. Magnification 1200. The rod-shaped sex chromosome and the supernumerary chromosome are seen lying off the metaphase plate.

Supernumerary chromosomes were present in all the southern samples of *Myrmeleotettix* but not in any of the samples from high altitude northern populations. These chromosomes were also found in a few individuals in two low altitude northern areas. Analyses showed that, within populations, those individuals with supernumeraries had significantly higher chiasma frequencies in the "normal" members of the chromosome complement than did those lacking supernumeraries. Further, no significant difference in chiasma frequency between the high altitude northern areas and the

southern areas was demonstrable in *Myrmeleotettix* when individuals with supernumeraries were left out of the analysis. It seems most likely that the supernumerary chromosomes have the effect of raising chiasma frequency in the other chromosomes (compare Mather, 1939) and that their presence is at least partly responsible for the higher chiasma frequencies of the southern populations of *Myrmeleotettix*. (It must be noted that any chiasmata between or within supernumeraries were ignored throughout the analyses.)

Supernumeraries were not found in *Chorthippus*, yet there were differences in chiasma frequency between the samples from the north and those from the south in this species, that were similar in magnitude to those found in *Myrmeleotettix*. It would seem that both species may have developed higher chiasma frequencies in the south and lower in parts of the north but that the regional differences have been produced by different mechanisms. That both species showed similar differences suggests that higher chiasma frequencies may be advantageous in the south (or lower frequencies advantageous in the north). It is therefore possible that supernumeraries were selected in the southern populations of *Myrmeleotettix* primarily because they affect chiasma frequency, or eliminated from the northern high altitude populations because they raise chiasma frequency.

4. CONCLUSION

The results reported are not extensive, but they do suggest that further study of chiasma frequency and supernumerary frequency in natural populations of these species would be well worth while. If such a study could be combined with ecological study to determine for example whether chiasma frequency in marginal populations (such as the high altitude populations of *Myrmeleotettix* may be) differs consistently from that in the more central populations (compare Carson, 1955) new understanding of natural populations might result.

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