

A STUDY OF THE INHERITANCE OF RECESSIVE COLOR
PATTERNS IN THE GRASSHOPPER LOCUST, PARATETTIX TENAXUS HANCOCK

by

EUGENE FRANKLIN OAKBERG

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INTRODUCTION AND REVIEW OF LITERATURE

The Tetriginae, or grouse locusts, are among the smallest of the Orthoptera. In addition to their small size, they are distinguished by the long pronotum which extends from the anterior margin of the prothorax back over the wings and abdomen. Pulvilli are lacking and the tegmina are greatly reduced or absent (Hancock, 1902; 1906-1907; Nabours, 1929). They are dimorphic with respect to wings and pronota (Nabours, 1929). In the short wing-pronotum form, which are unable to fly, the wings and pronotum extend to the distal ends of the femora of the jumping legs, the pronotum being slightly longer than the wings. In the long wing-pronotum form, the wings are longer than the pronotum and both extend 3-4 mm beyond the distal ends of the femora of the jumping legs. This latter form is able to fly, some of them considerable distances. Good (1941) reported this dimorphism to be inherited as a Mendelian pair of factors in Tettigidea parvipennis Harris, with short wings dominant. However, in Paratettix texanus Hancock and Apotettix eurycephalus Hancock, this difference in wing length is controlled by the environment.

More species have been found in North America than in Europe, and the largest numbers of varieties appear in the tropics. There is marked variation in the color

patterns, even within a species (Hancock, 1902, 1906-1907; Nabours, 1929).

The grouse locusts are usually found in moist woodlands or open spaces, especially near the banks of ponds, lakes and streams. Most of them feed on algae, lichens and humus (Hancock, 1902, 1906-1907; Nabours, 1929).

Twenty-four color patterns have been reported as dominant to the mottled gray +/+ pattern in Paratettix texanus. These patterns may be placed in five general groups: C, Cext, Cof, and Jof are white patterns showing on the anterior pronotum with mahogany to orange jumping leg femora; D and Dds are small white spots on the mid-dorsal region of the femora of the jumping legs; B, (white), N, N₁, and N₂, (brown), and Θ, (black), extend over the entire pronotum and jumping-leg femora; J, Hm, H, and I are spots that range in color from white to dark brown on the dorsal anterior pronotum; and K, S₁, S, Sm, E, L, P, and F are stripes that range from white to mahogany in color and extend lengthwise along the mid-dorsal pronotum and distal half of the jumping leg femora. (Nabours, 1914, 1917a, 1917b, 1923, 1929, 1930; Nabours and Foster, 1929).

All of the dominant factors except Θ are either allelomorphic or very closely linked and in this paper will be referred to as the dominant series. Hm crossed over once with each of the factors B, L, and S, a total of three times in 7,278 factor pairings, indicating that

it is very closely linked with the rest of the series (Nabours, 1929). The dominant factor θ is loosely linked with the other dominants, and crosses over with them to the extent of 47.58 percent in females and 25.34 percent in males (Haldane, 1920; Nabours, 1929).

Five other patterns; β , β^1 , sp, sf, and bl, all recessive to the +/+ or mottled gray pattern, have been studied in Paratettix texanus. In expression, β^1 is similar to β , but may be distinguished from β by the dull, brownish color of β^1 and the greater intensity of β over the anterior pronotum. Cypert (1932), reported independent segregation of β , β^1 , and sp with each other and with the dominant series and θ . The pattern sp, or white-specked all over, is a recessive. However, aberrant ratios were observed in the backcross and crosses between two animals heterozygous for sp. Tabor (1935), reported a ratio of 493 sp/sp : 660 + / sp from +/sp X sp/sp matings and a ratio of 138 sp/sp : 532 non-sp from +/sp X +/sp crosses. This significant deviation from the expected ratios has been attributed to lowered viability of animals homozygous for sp. The character sp shows 51.85 percent segregation with the dominant series and 55.34 percent with θ (Tabor, 1935).

Part of the present study concerns the inheritance of a newly discovered mutant gene designated as bl. Another object of this study was to test the hypothesis that Cypert (1932), and Tabor (1935), suggested regarding the heredity

of *sf.* Data involving β were augmented and previous studies on β were confirmed.

MATERIALS AND METHODS

The specimens used in these experiments came from stock that was collected by Dr. Robert K. Nabours near San Antonio, Texas, in 1938, 1939, and 1940. These animals have been bred in the laboratory since they were brought in from nature. In the greenhouse, Paratettix texanus will produce approximately four successive generations during the year, with more favorable growth during the months of March to June inclusive.

The natural habitat of these insects was simulated as nearly as greenhouse conditions would permit. The animals were reared in cages made by setting 8 x 12 inch glass cylinders in 10 inch pots containing sterilized sand and loam. To facilitate feeding and handling of the specimens, removable lids of 18-22 mesh screen were used. Filamentous and non-filamentous green algae were used as food for the grouse locusts, and the soil in the jars was kept moist. (Nabours, 1914, 1929, 1937).

A freshly prepared jar was used for each mating. Records were made of the date of the mating and the sources and genotypes of the male and female. These were written on a wooden tag which was placed in the mating cage with the animals. The breeding cages were checked daily, and as soon

as young were observed, the data were entered in the record books. The young were transferred to fresh jars, approximately 30 to each jar, where they remained until the third or fourth instar, when they were large enough to record. Matings were considered to be through producing offspring 30 days after the female had died, and the jars were then removed from the table and reconditioned for further use.

At about the fourth instar, the color pattern of each specimen was carefully recorded, and those individuals desired for mating purposes were segregated by sex and placed in fresh jars to mature. Specimens not used for the matings and adults that had finished breeding were placed in small bottles of 95 percent alcohol. Later, they were transferred to glass vials which were hermetically sealed, and kept for permanent records.

THE INHERITANCE OF β

The pattern β is a rusty-red color extending over the pronotum, body, head, and legs (Nabours, 1929, 1930; Cypert, 1932; Tabor, 1935). The present work confirms earlier observations that this color is due to the action of a recessive gene that is carried on a different pair of chromosomes from the dominant factors (Cypert, 1932). In the following discussion, individuals of the genotype β/β show the rusty-red while those of the genotypes $+/+$ or $+\beta$ do not. Most of the specimens showed at least one other pattern, but none of the known dominant or recessive factors is epistatic to β/β .

Table 1. Statistical analysis of data on the inheritance of β .

Genotype of parents	Number of matings	Total no. of offspring	Observed frequencies	Expected frequencies	Chi-square	Probability in percent
δ	ϕ		δ/β off-spring	δ/β off-spring		
δ/β x δ/β and recip.	56	2259	2259	2259	0	
δ/β x δ/β	79	2310	1681	1732.5	577.5	4.097
δ/β x δ/β and recip.	95	3643	1807	1821.5	1821.5	.230
δ/β x δ/β	9	201	0	0		

Table 2. Segregation of β from the dominant factors.

Segregation from dominant series	Genotype of parents	d	Number of matings	Total no. of gametes tested	No. gametes segregating	Percent segregation
Segregation from dominant series	$+/ \beta \times \beta / \beta$		19	648	328	50.62
	$\beta / \beta \times + / \beta$		22	827	372	44.98
Segregation from Θ	$+/ \beta \times \beta / \beta$		6	99	49	49.49
	$\beta / \beta \times + / \beta$		4	62	31	50.00
Totals			51	1636	780	47.67

Therefore, except in tests for linkage, it is possible to treat the data as if β and its dominant allelomorph, $+$, were the only genes involved.

Fifty-six $+/+$ x β/β matings produced 2259 progeny, none of which showed β , and all were of the genotype $+/+$ as expected (Table 1). From 79 $+/+$ x $+/+$ crosses, 1691 $+/+$ and $+/+$ and 620 β/β animals were recorded. The deviation from the expected ratio of three non β : 1 β/β is statistically significant, but the discrepancy is acceptable when the data from other pairings are considered. Ninety-five $+/+$ x β/β matings produced 1807 $+/+$ and 1836 β/β offspring, a very close agreement with the expected 1:1 backcross ratio. Nine β/β x β/β matings bred true, as all of their 201 progeny showed the pattern β/β .

Tests for linkage of β with Θ gave 49.49 percent segregation in males and 50 percent in females (Table 2). Data on linkage of β with the dominant series show 50.62 percent segregation in males and 44.98 percent in females. Therefore, these results indicate that β and all dominant factors assort at random.

From these studies, it may be concluded that the pattern β/β is due to the action of a recessive, autosomal gene which is carried on a different pair of autosomes from the dominant series and Θ (Cypert, 1932).

THE INHERITANCE OF bl

The recessive pattern bl/bl is a sooty black color that extends over the pronotum, abdomen, head, and legs. The tips of the jumping leg femora are black in both bl/bl nymphs and adults, but the black over the rest of the body does not become pronounced until after the last molt. The black tips on the femora of the jumping legs are, therefore, the only means by which bl/bl nymphs may be distinguished. The intensity of the pattern varies greatly. The bl/bl is sometimes so dark as to obscure the dominant patterns I, J, P, and S, especially when it occurs in combination with Θ . With Θ , the presence of bl may be determined by the black tips on the femora of the jumping legs and by the even distribution of bl over the entire specimen. The dominant allelomorph of bl is designated as +, and in the following discussion, animals of the genotypes +/+ and +/bl do not show the pattern. None of the other recessive or dominant factors is epistatic to bl/bl and, except in tests for linkage, they may be omitted from the summary of bl data.

Adults with the sooty black pattern were first observed among the offspring of a brother-sister mating. When a pedigree of these black animals was made, it was found that they were the descendants of a female brought in from San Antonio in 1939. This pedigree indicated in-

Table 3. Statistical analysis of data on the inheritance of bl.

Genotype of parents	Number matings	Total no.	Observed frequen- cies	Expected frequen- cies	Chi- square	Probability in Percent
σ			$\frac{+}{+}$ and $\frac{+}{bl}$ off- spring	$\frac{+}{+}$ and $\frac{+}{bl}$ and $\frac{+}{+}$ off- spring		
$\frac{+}{+} \times \frac{bl}{bl}$ and recip.	24	459	459	459	0	
$\frac{+}{bl} \times \frac{+}{bl}$	24	422	312	316.5	105.5	65
$\frac{+}{bl} \times \frac{bl}{bl}$ and recip.	31	803	408	401.5	401.5	66
$\frac{bl}{bl} \times$ $\frac{bl}{bl}$	9	131	0	0	131	

Table 4. Segregation of bl from the dominant series.

Genotype of parents	Number : matings	Number gametes : tested	Number gametes : segregating	Percent : segregating
$\frac{+}{bl} \times \frac{bl}{bl}$	8	248	170	68.55
$\frac{bl}{bl} \times \frac{+}{bl}$	6	191	92	48.16
Totals	14	439	262	59.68

heritance due to recessive genes, and it was assumed that specimens showing the pattern were of the genotype bl/bl and that those that did not show the pattern were of the genotypes $+/+$ or $+/bl$. Table 3 contains the data on bl , which support the theory that the pattern is due to the action of a recessive factor.

Twenty-four $+/+$ x bl/bl matings produced 459 progeny, all of them non-black and of the genotype $+/bl$ as expected (Table 3). The 312 non-black and 110 black specimens recorded from 24 $+/bl$ x $+/bl$ crosses are in close agreement with the expected ratio of 3 non-black : 1 black. The expected 1:1 backcross ratio was obtained, with 408 non-black and 395 black offspring recorded from 31 $+/bl$ x bl/bl pairings. Nine bl/bl x bl/bl matings bred true, as all of their 131 offspring were black and of the genotype bl/bl .

Tests for linkage of bl with the other recessives and dominants gave the following segregation values: with the dominant series, 68.55 percent in males and 48.16 percent in females; with ρ , 41.02 percent; and with θ , 47.62 percent. Data on linkage of bl with ρ and θ are insufficient for any conclusive statement, but the small numbers observed at the present time indicate random assortment of ρ , bl , and all the dominant factors. Such results may be due to very loose linkage, but if such were the case, one would expect less crossing over in males than in females as has been

observed in *Drosophila*, *Apotettix eurycephalus*, and with the factor Θ and the other dominants in *Paratettix texanus*.

The pattern bl/bl is due to the action of a recessive, autosomal factor that segregates independently of δ and also the dominant factors. This indicates that in the present stock of *Paratettix texanus*, three pairs of autosomes carry mutant genes. One pair of chromosomes carries Θ and the dominant series, one pair carries δ , and one pair carries bl .

THE INHERITANCE OF sf

The pattern sf/sf (specked femora) is a small, irregular white spot or group of white spots on the mid-dorsal region of the jumping leg femora. The pattern varies from a few scattered spots or a very small white spot to a bright pattern similar to the dominants D and Dds , white spots in the same position as sf (Nabours, 1914, 1929; Cypert, 1932; Tabor, 1935). The dominant patterns B , C , $Cext$, Cof , D , and Dds are either partially or completely epistatic to sf/sf . The extent of this pattern is decreased and its intensity increased by the presence of Θ , N and N_1 (Cypert, 1932; Tabor, 1935). In the summaries of sf , data that involve the patterns B , C , $Cext$, Cof , D , and Dds have been omitted. Although it varies in expression when present with different patterns, sf may be readily determined with all patterns except the six mentioned above.

The various specked femora, which have been designated by the common symbol *sf* are due to factors acting as recessives to $+/+$. A male and female, neither of which shows the pattern, will produce offspring that show *sf*. This led to the hypothesis that specked femora was due to the action of genes recessive to their wild-type allelomorph $+/+$. If this were true, animals with the pattern would be of the genotype sf/sf , and those without the pattern would be of the genotype $+/+$ or $+/sf$. Irregularities in the expression of *sf* suggested the presence of a recessive inhibitor or suppressor (*s*) of *sf* (Cypert, 1932; Tabor, 1935). Assuming the presence of an inhibitor, $sf/sf +/+$, $sf/sf +/s$, and sf/sf individuals have specked femora, and $+/+$, $+/sf$, $+/+ s/s$, $+/+ +/s$, and $sf/sf s/s$ specimens do not show the pattern.

From 25 $+/sf \times +/sf$ crosses, 668 non-*sf* and 459 sf/sf specimens were recorded, a ratio of 5 non-*sf* : 3 sf/sf instead of the 3:1 distribution expected (Table 5). The Chi-square test of significance shows that such a distribution would be expected less than one time in 1000, and indicates that the inheritance of *sf* involves more than a single recessive gene. The same 5:3 frequency was observed in the progeny of 97 $+/sf \times sf/sf$ matings, in which 2089 non-*sf* and 1285 sf/sf individuals were recorded. When the expected 1:1 ratio is used as the null-hypothesis, the probability of such a distribution occurring is less than one time in 1000. Eleven $sf/sf \times sf/sf$ combinations produced 273 non-*sf* and 99 sf/sf

Table 5. Statistical analysis of data on the inheritance of sf.

Genotype of parents	Number of matings	Total	Observed frequen-		Expected frequen-		Chi-square	Probability in percent
			offspring	Non-sf	spring	Non-sf		
δ	φ		sf	sf/sf	off-spring	off-spring	sf/sf	off-spring
δ /sf x φ /sf	25	1127	668	459	845.25	281.75	72.17	0.001
δ /sf x φ sf/sf	97	3374	2089	1285	1687	1687	191.57	0.001
δ sf/sf x φ sf/sf	11	372	99	273	0	372		

Table 6. Statistical analysis of data on the inheritance of a recessive suppressor (s) of sf.

Genotype of parents	Number matings	Total no. of offspring	Observed frequencies	Expected frequencies	Chi square	Probability in Percent
$\sigma \times \phi$			sf/sf x sf/sf s and recip.	Non-sf offspring	Non-sf offspring	
sf/sf σ / s/s ϕ	6	140	128	0	140	
sf/sf σ / s/s ϕ	15	371	182	249	96.75	12.52
sf/sf σ / s/s ϕ and recip.	24	775	350	425	387.5	7.16
sf/sf σ / s/s ϕ and recip.	18	445	367	58	445	0

offspring, a 3:1 ratio instead of all sf/sf animals as expected.

In the sf/sf x sf/sf matings mentioned in the previous paragraph, the presence of a recessive suppressor would give the observed 3:1 distribution and this suppressor would also explain some of the discrepancy noted in the +/sf x +/sf and +/sf x sf/sf crosses. If a recessive suppressor (s) were present, the non-sf progeny of sf/sf x sf/sf pairings should be of the genotype sf/sf s/s. Six sf/sf s/s x sf/sf +/+ matings produced 140 offspring, all of which should have been of the genotype sf/sf +/s and therefore should have shown the pattern, but 128 non-sf and 12 sf/sf were recorded (Table 6). Some deviation would be expected, as many of the sf/sf +/+ specimens may have been of the composition sf/sf +/s. However, if this were true, a ratio approximating 1:1 would be expected instead of the 11 non-sf:1 sf/sf distribution observed.

Theoretically, when two sf/sf +/s individuals are mated together, a ratio of 3 sf/sf:1 non-sf should be observed in their offspring. However, from 13 sf/sf +/s x sf/sf +/s matings, 122 non-sf and 249 sf/sf animals were recorded, a great discrepancy from the expected frequency of 3 sf/sf:1 non-sf. Twenty-four sf/sf +/s x sf/sf s/s crosses produced 350 non-sf and 425 sf/sf progeny, a statistically significant deviation from the expected 1:1 ratio. The distribution observed in the above data would be expected to occur less than

one time in 100. Eighteen supposedly sf/sf s/s x sf/sf s/s matings failed to breed true, as 58 of their 445 offspring had specked femora. These results indicate that all the discrepancies observed in sf data are not due to the action of a simple recessive suppressor of sf .

Upon the assumption that specked femora was due to the action of several genes, some sf/sf males were mated to females from stock that had not shown sf in five inbred generations. If more than one pair of chromosomes carried factors for sf , some of the gametes from the sf/sf parent should contain the complement of genes necessary to cause specked femora in the offspring. About one-fifth of the progeny showed sf . These results may be explained by the interaction of two dominant genes, one from each parent, to produce specked femora. The non- sf parent should have been homozygous, and all of the sf offspring from such crosses should be of a similar genotype. However, there was considerable variation in the expression of the pattern. Therefore, the more logical explanation appears to be that in the sf parent, there were several genes capable of affecting the expression of sf , and that in some of the gametes formed, there was present a complement of genes that would produce specked femora.

All of the matings that involved sf produced 2111 non- sf males; 1732 non- sf females and 1010 sf/sf males; 1748 sf/sf females. The numbers of non- sf and sf/sf females are approximately equal, but only 32.36 percent of the males had specked

femora. This deviation in the males suggests heredity involving sex. No evidence of sex linkage has been obtained. Therefore, an explanation involving sex-influenced inheritance has been favored, but no adequate interpretation of this discrepancy has been proposed at the present time.

These results indicate that the pattern sf/sf is not inherited as a simple recessive, the expression of which is influenced by a recessive inhibitor. The large number of males not showing the pattern, the great variation in size and intensity of the sf spot, and the failure of the specimens to breed true suggests the presence of several genes, the action of some of these genes being influenced by the sex of the individual in which they occur.

OTHER FACTORS STUDIED

In connection with the study of these recessives, nineteen of the previously reported closely linked or allelomorphous dominants, and the loosely linked dominant Θ were utilized (Nabours, 1914, 1917a, 1917b, 1923, 1929, 1930; Nabours and Foster, 1929). However, since nothing new of importance was ascertained, the data dealing with the dominants were omitted.

SUMMARY

1. A newly discovered recessive color pattern, $b1/b1$ and further studies of the recessive color patterns β/β and

sf/sf in Paratettix texanus Hancock are described in this paper. Except in tests for linkage with the recessives, the data on the dominant factors have been omitted.

2. The pattern ϕ/ϕ is inherited as a recessive, autosomal gene that segregates independently of the dominant factors and *bl*.

3. The pattern *bl/bl* is inherited as a recessive, autosomal gene that assorts at random with the dominant factors and ϕ .

4. Specked femora, *sf/sf*, is probably due to the action of several genes, with the expression of some of them influenced by the sex of the individual. Also, a suppressor of some of the *sf* genes may be present.

5. Specked all-over, *sp/sp*, which is described in the introduction, is inherited as a partially lethal, autosomal recessive that segregates independently of the dominant factors.

6. In the present stock of Paratettix texanus Hancock three pairs of autosomes carry mutant genes. One pair of chromosomes carries the dominant factors, one pair carries ϕ , and one pair carries *bl*.

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