

THE INHERITANCE OF TWO RECESSIVE COLOR PATTERNS,
(SP AND SF) AND A SUPPRESSOR (S), IN THE GROUSE
LOCUST, PARATETTIX TEXANUS HANCOCK

by

MARGARET JEANNE TABOR

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INTRODUCTION AND REVIEW OF LITERATURE

This paper deals with (1) the description and linkage relations of the recessive elementary color pattern white-specked-all-over (sp); (2) the aberrent ratios which indicate the lowered viability of sp/sp individuals; (3) the

description of the variable recessive white-specked-femora (sf); and (4) the presence of a recessive suppressor (s) of sf/sf which accounts for the failure of the homozygotes to breed true in some instances.

The grouse locusts are among the smallest of the Orthoptera. The large pronotum covers the meso- and meta-notum, extending back either to the distal ends of the femora of the jumping legs or somewhat beyond that point. The wings, which may be comparatively large and well-developed, generally correspond in length with the pronotum which covers them. Pulvilli are lacking and tegmina are greatly reduced or absent (Hancock, 1902; Nabours, 1929).

Paratettix texanus was first described as belonging to the sub-family Tettiginae of the family Tettigidae (Hancock, 1902). It was later placed in the sub-family Tetrigininae and family Acridiidae (Hancock, 1906) which seems to be its position at the present time¹. Taxonomists are apparently not fully agreed on the specific name.

Twenty-three dominant and four recessive elementary color patterns, as well as the gray mottled "wild-type", have been described (Nabours, 1914, 1917, 1923, 1929, 1930; Nabours and Foster, 1929; Cypert, 1932). The

¹Unpublished letter from A. N. Caudell, U.S.D.A., Bureau of Entomology, Washington, D. C.

dominant patterns consist of a variety of pronotal spots and stripes as well as general colors. The recessive patterns (sp and sf) with which this paper deals have been briefly described (Nabours, 1929; Cypert, 1932) and the possibility of a suppressor of sf pointed out (Cypert, 1932). The other two recessives, ϕ and ϕ' , resemble each other rather closely but a distinction can be made between them. ϕ has a pronounced reddish cast of varying degrees of intensity on head, legs, pronotum and abdomen. ϕ' is not quite as pronounced anteriorly, is browner and has less luster than ϕ (Cypert, 1932).

The wild type seems to act as the recessive allele of the dominant patterns and the dominant allele of the recessive ones. Twenty-one of the dominant elementary color patterns, which are referred to as the series, are either extremely closely linked or allelomorphic since no crossing-over has ever been observed among them. The twenty-second, Hm, which is very closely linked with the series has crossed over only three times out of a total of 7,278 factor pairings. θ , the twenty-third dominant factor, is loosely linked with the series and has a cross-over value of 25.34 per cent in the males and 47.58 per cent in the females (Nabours, 1929).

Specific suppressors occur in various animals but probably more have been reported in Drosophila melanogaster than in any other one. It has been demonstrated that the suppression of morula, speck and balloon in Drosophila melanogaster is due to a duplication of a portion of the III chromosome (Bridges, 1919; Schultz and Bridges, 1932). Black-suppressor is a sex-linked recessive which shows variability in its effects since a few flies in most suppressed-black cultures show a light black trident on the posterior part of the thorax (Plough, 1927). Two allelomorphic recessive suppressors of purple have been located in the third chromosome (Bridges, 1932). The suppressor of Hairy-wing, port-suppressor and the suppressor of vermilion and sable have all been described as recessives (Schultz and Bridges, 1932; Bonnier, 1926). Spineless-Suppressor, a dominant factor on the third chromosome, is lethal when homozygous. In the heterozygous form it turns the homozygous ss (spineless) into the wild type except for the posterior scutellars which remain small (Morgan, Bridges, Sturtevant, 1925).

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MATERIALS AND METHODS

The specimens used in these experiments were taken from the stock of Paratettix texanus which has been bred in the greenhouse for some time. These animals have been secured chiefly in southern Louisiana and Texas, usually near streams or fresh water ponds. This southern form has no hibernation period and will produce as many as four generations a year if the greenhouse temperature approximates that of their natural habitat. March to June, inclusive, seems to be the most favorable breeding season and the two generations produced during this period greatly outnumber the two which are secured during the remainder of the year.

The cages consist of 8-inch by 12-inch pyrex cylinders set in tile bulb pots which are filled with steam-sterilized sand and loam. The lids are formed of 16 to 24 mesh screen wire. The food consists mainly of filamentous algae (Nabours, 1914, 1929).

A single pair of grouse locusts is placed in each mating jar. After copulation the female deposits the eggs in the soft soil which is kept rather moist to simulate their natural environment. About three weeks later off-

spring begin to hatch and are then transferred by mechanical means to renovated cages (Nabours and Millenbruch, unpublished paper).

During the third or fourth instar the phenotypes of the young grouse locusts are recorded in conjunction with those of the parents. Males and females are then separated and placed in freshly prepared jars. As the offspring become adult they are used for further matings. Those which are not mated are again recorded, preserved in 95 per cent alcohol and later hermetically sealed in glass vials. Parents are preserved in the same manner when they have finished breeding.

EXPERIMENTAL DATA

Inheritance of the Elementary Recessive Color Pattern White-Specked-All-Over (sp)

Description. The pattern known as white-specked-all-over, which consists of white specks, or mottling, over the entire dorsal surface, head and legs, is designated as sp/sp for the homozygote and +/sp for the heterozygote, the + representing the dominant allele of sp. Homozygous specked tends partially to obscure some patterns of the dominant series such as H, a yellow or orange pronotum spot; Hm, a lighter spot in the same position as H, and L,

which consists of three yellowish white lines along the pronotum and one along the femora of the third pair of legs. Others of the series, particularly pronotal stripes, may be easily distinguished through the specking. e, which is an intense black all over the animal, diminishes the number of white spots and decreases their size considerably. Both B and Cof offer a white or grayish background with which the white specks do not show well. For this reason they may be considered as partially epistatic to sp even though they do not affect the size or number of spots. However, as far as our observations have gone, all sp/sp individuals can be distinguished with any pattern. It is neither completely epistatic nor hypostatic to any other pattern.

When the pattern was first noticed it was thought to be a mutation which had occurred in the greenhouse. However, subsequent and more complete data indicate that it was probably brought in from nature in a heterozygous condition and was carried for two generations before proper matings produced a homozygote and thus enabled it to appear.

All sp/sp individuals can be traced back to a female collected October 7, 1930, at San Antonio, Texas. Later generations tend to substantiate that she, rather than the

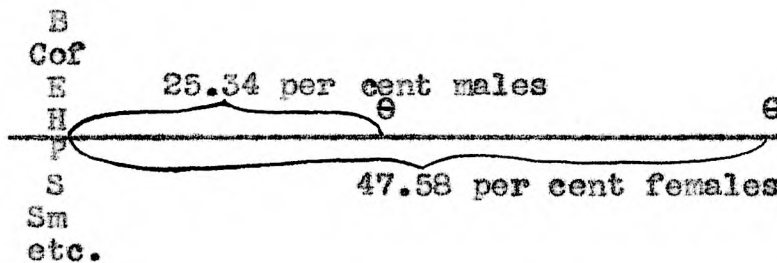
male to which she was mated, carried the pattern, since many of his brothers and sisters showed, when tested, that they did not carry the sp.

The expression of the pattern is clearly due to a recessive gene. Although many of the sp/sp x sp/sp matings failed to produce offspring, three successful matings of this type gave thirty offspring of the composition sp/sp.

The numbers are small, yet they indicate that the homozygous recessives (sp/sp) breed true. Examples can be cited in which a pair of non-specked individuals, both heterozygous for the factor, produced approximately one-fourth sp/sp offspring. In all heterozygotes observed sp seems to be completely recessive to its normal allele.

Linkage Relations. Linkage relations indicate that sp is on a different pair of chromosomes from that of the series and θ . The twenty-one dominant elementary patterns of the series, which are either extremely closely linked or alleles, were considered as having a single locus in order to determine linkage relationships. The loosely linked θ has a cross-over value with the series of 25.34 per cent in the males and 47.58 per cent in the females.

Chromosome Map

Series

When sp was tested with the series there were 108 non- to 111 segregates, or 50.68 per cent of segregation in the males, and 255 non- to 280 segregates, or 52.53 per cent of segregation in the females. With θ sp gave 28 non- to 32 segregates, 53.33 per cent of segregation in the males, and 64 non- to 82 segregates, 56.16 per cent of segregation in the females (Table 1).

It seems peculiar that in all cases there is slightly more than 50 per cent of segregation, but this excess does not appear to be significant. Since crossing over occurs much less frequently in the males than in the females the fact that there is approximately 50 per cent of segregation for both indicates the independent assortment of sp with the series and θ . This conclusion is further strengthened by the fact that segregation with the loosely linked θ is practically the same as with the series. This would

Table 1. Segregation Table for sp.

Factor	Males			Females			Totals		
	:Non-segregates	:Segregates	:Per cent of segregation	:Non-segregates	:Segregates	:Per cent of segregation	:Non-segregates	:Segregates	:Per cent of segregation
B	11	14	56	16	11	40.74	27	25	48.07
E	34	35	50.72	64	79	55.24	98	114	53.77
H	1	5	83.33	30	36	54.54	31	41	56.94
Jm	11	9	45	9	4	30.77	20	13	39.39
K	1	1	50	26	33	55.93	27	34	55.73
L	18	15	41.93	24	39	61.90	42	52	55.32
Sm	29	32	52.46	40	44	52.38	69	76	52.41
Cof	3	2	40				3	2	40.00
+	—	—	—	<u>46</u>	<u>34</u>	<u>42.50</u>	<u>46</u>	<u>34</u>	<u>42.50</u>
Total for series	108	111	50.69	255	280	52.33	363	391	51.85
θ	28	32	53.33	64	82	56.16	92	114	55.34
Total for series and θ	136	143	51.25	319	362	53.15	455	505	52.60

certainly not be the case if sp were on the same pair of chromosomes. Totals for the series and θ show 455 non- to 505 segregates, or 52.6 per cent of segregation.

Aberrent Ratios Showing the Lowered Viability of Homozygous Specked Individuals. A significant deficiency of specked (sp/sp) individuals has been noted. From matings of sp/sp males to +/sp females and the reciprocal matings, a 1 to 1 ratio of sp/sp to +/sp offspring would be expected. However, matings of this type produced 493 sp/sp to 660 +/sp individuals, a significant deviation of 7.28 times the probable error from the expected 1 to 1 ratio. Matings of heterozygotes (+/sp x +/sp) produced 138 sp/sp to 532 non-specked (+/sp and +/+) offspring. Although the deviation of 3.91 times the probable error is not necessarily significant it is in the same direction as in the matings of homozygotes to heterozygotes. Matings made during the same period and involving the color pattern ϕ which, like sp, is an autosomal recessive factor, have been used for controls. ϕ/ϕ x +/ ϕ and the reciprocal matings gave 1058 ϕ/ϕ to 1015 +/ ϕ offspring, a 1 to 1 ratio; +/ ϕ x +/ ϕ matings produced 491 ϕ/ϕ to 1400 non- ϕ (+/ ϕ and +/+) animals, a 3 to 1 ratio, all without significant deviation.

The aberrant ratios secured from matings in which *sp* was involved indicate that for some reason which is not yet known homozygous specked individuals have a lower viability than non-specked, heterozygous sibs. The presence of a lethal linked with *sp* cannot be definitely determined until other factors are found in the same linkage group. Another possibility is that the *sp* factor may have multiple effects and, in addition to producing the specked pattern, may cause a general weakening and the resultant death of some individuals. The difficulty of securing productive *sp/sp* x *sp/sp* matings seems to support the latter idea. It has been shown in *Drosophila* that generally the more widely a factor deviates from the wild type the less viable are the insects carrying it. Since the *sp* pattern is one of the most striking found in *Paratettix texanus* the same generalization may hold true for it.

Inheritance of the Recessive White-Specked-Femora (*sf*) and Its Suppressor (*s*)

Description of Specked-Femora. The *sf* pattern consists of a small white dot or a localized group of white spots at the midpoint of the inner dorsal surface of each hind femur. These markings vary decidedly in intensity and extent. Some (*sf/sf*) are exceedingly bright,

relatively large and often associated with a white marking on the anterior part of the pronotum (specked anterior pronotum); others show plainly and are of medium size but do not have the intensity of sf/sf; still others are rather small but fairly clear and offer no particular difficulties in recording. In addition there are the variations caused by the other patterns with which sf occurs. The gray, mottled "wild-type" (+/+) K, L, H, Hm, Jm, N, N₁ and P do not affect its expression to any great extent. E, S, and Sm all have a certain amount of color on the hind femora which tends to make the sf appear as a narrow line rather than as a dot or compact group of spots. Θ, which cuts down the size considerably but does not affect the intensity, causes it to appear as one or more small bright dots. Both the large bright sf/sf and the moderately strong one show distinctly through the white of the B and sp patterns but the small, less pronounced marking is difficult to record correctly when it is associated with those patterns. The orange femora of Cof, the reddish mahogany femora of Cext, and the prominent white femoral spot, D, entirely cover the sf.

The sf pattern has previously been described as a recessive (Nabours, 1929; Cypert, 1932). Numerous citations can be made of matings in which neither parent

showed the sf but approximately one-fourth of the offspring showed it. Totals from a number of $+/sf \times sf/sf$ and $sf/sf \times +/sf$ matings gave 2355 sf/sf to 1360 $+/sf$ offspring. The significant deviation from the expected 1 to 1 ratio is 7.66 times the probable error. Here again, there is the possibility of a lethal or sub-lethal but it seems more probable that the irregularity may be due to complications caused by the presence of a suppressor of sf. Numerous $sf/sf \times sf/sf$ matings have been observed to breed true but it was in this particular type of mating that aberrations in the inheritance of the pattern were first noted. Occasionally parents which both had a bright sf produced offspring, some of which did not show the marking but when bred further proved to be of the composition sf/sf . This peculiarity of behavior was found to be due to the presence of a recessive suppressor (s) which varies slightly in its effects.

Occurrence of the Suppressor. In some cases the suppressor completely inhibits the expression of the sf; in others it allows slight traces to appear. Occasionally animals show the sf slightly when they are recorded as nymphs but fail to show it when they become adult. From matings in which both parents had a distinct sf but were heterozygous for the suppressor 684 offspring showed the

sf without any doubt and 217 were suppressed, which is very close to a 3 to 1 ratio. From s/s x +/s and the reciprocal matings a total of 175 +/s to 152 s/s offspring were obtained, an acceptable 1 to 1 ratio. Matings of "suppressed" individuals to those not carrying the suppressor (+/+) produced 183 offspring, all of which showed a clear sf. Those of the 183 which were bred further proved to be of the composition +/s. Matings of the types cited above have also shown that the suppressor is an autosomal factor since all the offspring showed a prominent sf whether the suppressed parent was the male or female. Results of critical s/s x s/s matings have been obscured in many cases by the presence of the color patterns B or sp. From one clear-cut mating of this type only four individuals, all showing the effects of the suppressor, were obtained.

Linkage Relations of sf. Due to the presence of s, linkage relations of sf have been difficult to determine. However, Table 2 gives some data for the females. When sf was tested with the series there were 427 non- to 428 segregates, or 50.05 per cent of segregation. With 6 there were 198 non- to 165 segregates, 45.45 per cent of segregation (or linkage). This is within the possible range of independent assortment since the deviation from a 1 to 1

ratio is only 2.85 times the probable error. The fact that *sf* shows practically independent assortment with both the series and θ , which are very loosely linked, indicates that it is on a separate pair of chromosomes from them.

Table 2. Segregation Table for *sf* Females

<u>Factor</u>	<u>Non-Segregates</u>	<u>Segregates</u>	<u>Per cent of Segregation</u>
+	2	4	33.33
B	1	0	0
C	3	0	0
F	45	86	65.64
H	5	2	28.57
J	107	31	22.46
K	107	168	61.09
L	126	79	38.53
M	26	47	64.38
Sm	<u>5</u>	<u>11</u>	<u>68.75</u>
Total for Series	427	428	50.05
θ	198	165	45.45

Two facts seem to show the presence of modifying factors other than the suppressor: (1) The great amount of variation found among distinct sf markings and (2) the variation found among "suppressed" individuals, some of which show slight traces of sf although others show no sign of it.

SUMMARY

1. The recessive elementary color pattern sp has been found to be on a separate pair of chromosomes from that of the series and θ .
2. A significant deficiency showing lowered viability of sp/sp individuals has been noted.
3. An autosomal recessive suppressor (s) is responsible for some of the irregularities of inheritance associated with sf.
4. The data available indicate that sf, as well as sp, is on a separate pair of chromosomes from that of the series and θ , but data are not available for ascertaining whether or not sp and sf are on the same pair.
5. Modifiers of sf other than the suppressor seem to be present.

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