A STUDY AND SUMMARY OF THE INHERITANCE OF THE COLOR PATTERNS IN THE GROUSE LOCUST PARATETTIX TEXANUS HANCOCK

by

GRACE JUANITA YESLEY

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HISTORY AND DESCRIPTION OF GROUSE LOCUSTS

Hancock (1902) first described Paratettix texanus as belonging to the sub-family Tettiginae of the family Tettigidae. It was later placed in the sub-family Tetriginae and family Acrididae (Hancock, 1906).

As early as 1767, Linnè used the term Bulla as the sub-family name. Scudder and others used such names as Tettix, Tettiginae, Tettigidae and Tetriginae. The common names for these grasshoppers are grouse, pygmy or swamp locusts (Nabours, 1947).

These locusts are among the smallest of the Orthoptera, attaining a length of approximately one-half inch. They are characterized by an extremely well developed apical process of the pronotum which extends backward over the mesonotum and metanotum and to either the end of the abdomen or a distance beyond the abdomen (Nabours, 1917, 1929, 1947).

The grouse locusts have a tendency toward being dimorphic with respect to length of wings and pronota. However, intermediate stages between the two extremes have also been noted (Nabours, 1917, 1929, 1947).

The grouse locusts normally inhabit moist areas, usually around fresh water lakes, ponds or the banks of streams. They have not been located any place which is affected by salt water. Paratettix texanus, the species with which primary concern rests in this paper, is most frequently found in open areas, along the algae-covered margins of ponds, especially as the water recedes in summer and fall. This species inhabits suitable areas mainly in Louisiana, Texas and Southeastern Mexico.

Paratettix texanus and the other grouse locusts feed on algae growing on moist soil or the filamentous algae at the line of fresh, receding water. In

southern Texas and Louisiana P. texanus is active the year round and normally has four generations per year; whereas northern species such as Acrydium arenosum, a species living in and around the region of Manhattan, Kansas, produces only one and one-half generations in the same period of time. The individuals of P. texanus are relatively inactive at temperatures below 50°-60° F. but quite active at temperatures above 70° F. in the shade. In greenhouses in the north, the southern species will continue to have four generations per year even though the northern species under similar circumstances will have no more than when out in nature (Nabours, 1917, 1929, 1947).

In 1908, specimens of P. texanus were collected at Houston, Texas and bred in greenhouses at the University of Chicago. In 1910, Nabours moved his grasshoppers to the Kansas State Experiment Station (Nabours, 1947). He has added new specimens from time to time to acquire different color patterns. Recently, the P. texanus died when the greenhouses were sprayed to rid them of insect pests.

METHODS AND MATERIALS

In raising Paratettix texanus in captivity, the most successful method employed thus far has been to use cages made of heavy glass cylinders 9" x 15" set in tile bulb pots 11" x 5" which were filled with sandy loam that had previously been steam sterilized. A small (4" x 4") flower pot with the hole plugged was placed upside down in the center of the bulb pot before the dirt was put in place. This type of cage permitted aeration for the soil and the inverted flower pot also provided a dry retreat. Food has in later years been placed directly on the soil to prevent drying out, which occurred previously when it was placed on the bottom of the flower pot. The dirt in the pots was kept moist at all times in order to simulate the natural habitat.

The lids of the cages were made of 20-24 mesh screen wire (Nabours, 1914, 1929).

Since the individuals of P. texanus do not normally hibernate during any season of the year, the temperature in the greenhouse, which is as near as possible that of the temperature in Louisiana and Texas, has enabled the grasshoppers to produce the expected four generations a year.

All parents and offspring have been carefully recorded according to color pattern and source so that a pedigree for any color pattern existing in the greenhouse is easy to obtain. Pairs of males and females of known origin were placed in jars, eggs were laid in the soil and, upon hatching, the offspring were transferred by means of a suction machine (Needham, 1937; Nabours, 1947) to new cages. They remained in these until the fourth instar when records were made of the color patterns. If any example of color patterns was not desired for further mating, those grasshoppers were preserved in 95 per cent alcohol in vials. Parents also were preserved in vials which were sealed hermetically with a torch.

DESCRIPTION OF THE COLOR PATTERNS

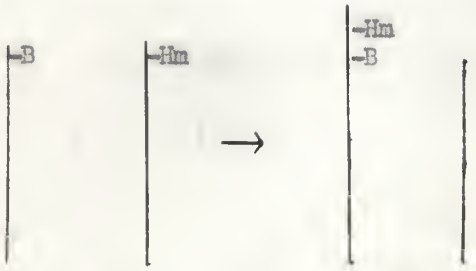
The "wild type", +/+, is characterized by a mottled gray which is regarded as the recessive. There are twenty-three genes for dominant color patterns which are either very closely linked or are multiple allelomorphs. They are all dominant over the "wild type" and incompletely dominant in relation to each other. These patterns may be described as follows: (1) B/B, white both on the pronotum and parts of the posterior femora; (2) C/C, white on the anterior pronotum with the pronotum dark or mottled and with reddish-brown legs; (3) Cext/Cext, almost the same as C/C except for an extension of the white of the anterior pronotum posteriorly and the line between the white anterior and dark posterior is not sharply defined; (4) Cof/Cof, the

same as C/C except for red middle legs and orange colored metafemora; (5) D/D, the same as +/+, but with conspicuous white spots on metafemora; (6) Dds/Dds, two small white spots on the mid-dorsal region of the metafemora; (7) E/E, broad yellow stripes along the median pronotum and distal ends of posterior femora; (8) F/F, broad mahogany stripes along the median pronotum and posterior femora; (9) H/H, large yellow or orange spot covering the same area as the white spot of J/J; (10) Hm/Hm, a gray, slightly orange spot covering the same area as the spot of H/H; (11) I/I, a dark mahogany spot covering the same area as that of J/J.

(12) J/J, large white spot over broad part of pronotum; (13) Jof/Jof, the same as J/J but with prominently orange colored metafemora and red middle legs; (14) K/K, narrow white stripe along the median pronotum and red middle legs; (15) L/L, three nearly white lines along the pronotum and one along the metafemora; (16) M/M, brown all over the pronotum; (17) N/N, a brown-gray all over; (18) N_1/N_1, dull orange all over; (19) N_2/N_2, brilliant orange all over; (20) P/P, broad brown stripes along median pronotum and on distal ends of metafemora; (21) S/S, broad yellowish, gray-white stripes along median pronotum and on the distal ends of the metafemora; (22) Sm/Sm, broad brown, slightly red stripes along median pronotum and on distal ends of posterior femora; (23) S_1/S_1, broad nearly clear white stripes along median pronotum and on distal ends of metafemora and with red middle legs. (Nabours, 1929). Other patterns have been collected, but they have not yet been analyzed sufficiently.

In Hm/B individuals the Hm has crossed over to the chromosome with B one time in spermatogenesis and one time in oögenesis out of a total of 4882 gametes. In BHm/A individuals, repulsion was noted once in males and twice in females out of 3396 gametes formed. Nabours (1929) concluded from

the data then available that the series are merely very closely linked and are not all allelomorphic. However, if considered as only closely linked genes, the crossover value (1929) would be less than .07 per cent. Since 1929, there have been no crossovers. This indicates that the percentage of crossing over is even smaller. An alternative explanation would attribute the apparent linkage between B and Hm to a duplication by mutation on the part of the chromosome containing the Hm factor on the chromosome with the B, as indicated in the following diagram. The loci of the gene Hm and its duplicate might be on either side of the locus of B.



This theory does not offer any reason for the "duplication" occurring twice between the B and Hm and not at all between the other genes in the series except when the Hm crossed to another chromosome from the one with the B. In reviewing these facts, the writer has concluded that the group of genes B, C, D, et al. are multiple allelomorphs or at least closely enough linked that there is no crossing over. The two original, apparent "crossovers" between B and Hm may be considered to have been due actually to translocations and the subsequent crossovers which resulted from an abnormal chromosome; one with two different genes which were allelomorphic.

Since there is no normal crossing over between genes of the series of dominants, all of them may be grouped and dealt with as a unit, A, when studying the relationship between these genes and others which are not included within the series.

Another gene, θ, which is dominant and epistatic to +/+ and is incompletely epistatic to the other patterns described, is characterized by the extension of black over the entire pronotum and metafemora (Nabours, 1929).

There are, in addition, some patterns which are inherited as recessives; (1) ϕ/ϕ, reddish or pink all over (Nabours, 1929); (2) ϕ'/ϕ', dull red all over (Cypert, 1932); (3) spk/spk, specked all over (Cypert, 1932); (4) bl/bl, a sooty black color that extends over the pronotum, abdomen, head and legs, black on the tips of the metafemora both in nymphs and adults, the black over the rest of body not pronounced until after the last molt (Oakberg, 1942); (5) sf/sf, white spots on the metafemora, resembling D/D, but recessive in heterozygotes and not showing well, even in some homozygotes in connection with a few patterns such as C, Cof, Jof (Nabours, 1929). There are probably a few or several different genes, all of which produce patterns of the appearance of sf. It has been recorded as having a recessive suppressor, s/s, but this has not been fully confirmed. This is apparently a complex problem yet to be solved, and it will require more matings and study to determine definitely the mode of inheritance.

θ was reported by Nabours (1914, 1917) as segregating independently of the A series. However, Haldane (1920) showed that there was actually about 23.6 per cent of segregation in the males and 46.2 per cent in the females. In 1929, Nabours with more data available reported that the percentage of crossing over in males was 25.34 and was 47.58 in females. With twice the data Nabours had at that time the percentage has now been found to be 25.55 and 47.54, respectively (Table 1).

Haldane (1920) reported this type of linkage to be intermediate between the type found in Drosophila and Bombyx, where no crossing over occurs

in the digametic sex, and the type found in most plants and mammals where the linkage is approximately equal in the two sexes. Crossing over in the males also does not occur in Apotettix eurycephalus, another species of the Tetriginae which has been bred and reported on extensively (Nabours, 1919, 1925; Nabours and Stebbins, 1950).

PRODUCTION OF THE TABLE

Testing for linkage between θ and A was rather simple because the genes, with the exception of +, are incompletely dominant with one another. The essentials necessary to make this test in the male are:

1. the male must be heterozygous for θ and the A series
2. the female must be homozygous recessive for θ

The reciprocal holds true for testing linkage in the female. An example of this type is a mating in which one parent received Cof and θ from one parent and B from the other parent. Genotypically, for example, the parents would be recorded as follows:

Parents	B/Cofθ x D/Jof		
Offspring	B/D	}	Non-crossovers
	B/Jof		
	Cofθ/D		
	Cofθ/Jof		
	Bθ/D	}	Crossovers
	Bθ/Jof		
	Cof/D		
	Cof/Jof		

This would test crossing over in the left hand parent. A reciprocal cross would test it in the other parent.

Testing for linkage between two recessives is more complicated. The requirements necessary to have proof of segregation or nonsegregation are as follows:

1. one parent must be homozygous recessive for both genes. (ø/øbl/bl)

2. the other parent must be heterozygous for both genes with proof that the two recessives came from the same parent. That is

Parents +/+ +/+ x ø/ø bl/bl

Valid offspring for test +/ø +/bl

Test cross +/ø +/bl x ø/ø bl/bl

In the foregoing mating, crossing over would be tested in the left hand parent.

Table 1. Segregation among genes.*

	Males					Females			
	Total Gam.	Non-Seg.	Seg.	Per cent Seg.		Total Gam.	Non-Seg.	Seg.	Per cent Seg.
Aθ**	29148	21699	7449	25.55	Aθ**	30699	16206	14593	47.54
Aϕ	3272	1688	1594	48.72	Aϕ	2344	1263	1081	46.11
Asf	1751	1029	722	41.23	Asf	860	528	332	38.60
Abl	869	462	407	46.84	Abl	943	497	446	47.51
Asp***	105	56	49	46.47	Asp***	101	51	50	49.50
θϕ	499	236	263	52.71	θϕ	482	249	235	48.76
θbl	9	6	3	33.33	θbl	127	69	58	45.66
θsf	452	266	186	41.15	θsf	220	120	100	45.45
ϕbl	411	243	168	40.88	ϕbl	233	177	56	24.03
ϕsf	395	216	179	45.32	ϕsf	0	0	0	?

* The author has included the data obtained since 1940 when Oakberg's thesis was written.
** Material before 1929 was summarized by Nabours and added to that summarized by the author since 1929.
*** Material was summarized by Oakberg in its entirety.

RESULTS DERIVED FROM THE TABLE

It is apparent that θ is linked with A (the dominant series): at least one of the sf determining genes is linked with the dominant series; ϕ and bl are linked to one another but not to the dominant series or θ. Oakberg (1942) reported that ϕ and bl were not linked. However, this conclusion came from insufficient data. The data would indicate that sp is not linked to A. There are no records testing the linkage relationships between sp and ϕ or sp and bl.

Since it has already been stated that possibly a number of undetermined genes are responsible for the sf characteristic, sf will not be dealt with to any extent at this time because the true crossover value between the A series and the sf gene which is linked with the series is impossible to determine.

The differences in crossover value in males and females between the A series and θ and between ϕ and bl has presented a considerable problem. It may be explained by a number of theories of which any, all, or none may be correct.

1. Since there are thirteen chromosomes in the males and fourteen in females, the x chromosome may carry a gene which when in the homozygous condition (normally only occurring in females) causes the synapsis to be more complete between the chromosomes carrying θ and A and less complete between the chromosomes carrying ϕ and bl.

2. The extensiveness of the synapsis may be regulated by cytoplasmic genes which have previously been produced or brought into action by the x chromosome.

3. The excess heterochromatin in the female may cause the differences in crossing over.

4. In some invertebrates, the presence of one organ is necessary for the development of another. In the female Gammarus the eggs are held in the brood-sac, after they are laid, by long bristles on the oöstegites. These bristles do not develop if the ovary fails to develop. And, in Asellus the brood-sac develops at the moults before the eggs are laid; it does not develop if the ovary has been destroyed. These facts strongly suggest that the development of the brood-sac in these animals is controlled by the gonad, and, if so, the control is probably by an internal secretion of the gonad, much as the secondary sexual characters of the vertebrate are

controlled. A few other examples of the dependence of one organ on the presence of another are known in invertebrates (Carter, 1940).

With the foregoing in mind, one might conclude that a sex hormone is responsible for the unequal crossover values found in males and females in Paratettix texanus. That is, perhaps a sex hormone influences the flexibility of chromosomes or the proximity of synapsis in the two pairs of chromosomes concerned—those with A and θ and those with ϕ and bl.

Another fact should be noted from the table. Only once was the segregation value more than fifty per cent. This may be significant but has not as yet been explained. To the knowledge of the writer, this has not been observed to occur in other organisms.

SUMMARY

1. θ and the "dominant series" are linked with 25.55 per cent crossover in males and 47.54 per cent in females.

2. θ and one gene for sf and the "dominant series" and one gene for sf are linked but the percentage of crossing over cannot be determined because of the complexity of the inheritance of sf.

3. ϕ and bl are linked with 40.88 per cent crossing over in males and 24.03 per cent in females.

4. All percentages of segregation except that between 0 and ϕ in the male are less than fifty per cent.

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