THE GENETICS OF THE GROUSE LOCUST TETTIGIDEA PARVIPENNIS HARRIS

by

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INTRODUCTION

The value of grouse locusts as genetic material has been indicated by Nabours (1925). The species, Tettigidea parvipennis Harris may have even greater significance than Paratettix texanus Hancock or Apotettix eurycephalus Hancock since it forms rather an intermediate step between the noneconomically important grouse locusts and the larger agricultural pests, which are unsuitable for rapid genetic exploration. The latter also are characterized by a complement of 23 (♂) and 24 (♀) chromosomes, while in the former there are 13 (♂) and 14 (♀) chromosomes (Robertson, 1916).

The approach to theoretical genetics by means of grouse locusts was begun by Nabours in 1908 (Nabours, 1914). Early taxonomic and natural history work was done on the species Paratettix texanus. Color patterns were used as the markers by which the transmission of parental chromosomes was deduced. Up to the present, thirty-one patterns have been reported in Paratettix texanus (Nabours, 1937). Nabours also indicated the inheritance of nineteen color patterns in the species Apotettix eurycephalus. A particularly close parallel between these two species was the fact that most of the genes for color patterns in each were found on one pair of chromosomes, respectively.

Of especial interest was the fact that these species reproduced parthenogenetically (Nabours, 1919, 1925, 1937; Nabours and Foster, 1929). One peculiarity was the production of males from homogametic females. The most likely explanation

for these males was that advanced by Robertson (1931) of non-disjunction of the female X-chromosome, producing a gamete without an X-chromosome which likely fused with a normal gamete. Color patterns apparently segregated normally.

Of further significance in Apotettix eurycephalus is the crossing over which occurs principally in the female, while in Paratettix texanus a limited amount of crossing over occurs in both males and females.

By x-raying, two translocations of sections of chromosomes carrying genes for several color patterns have been induced in Apotettix eurycephalus, one from autosome number 1, to number 4, and the other from number 1 to the sex-chromosome (Nabours and Robertson, 1933; Nabours and Stebbins, 1935; Robertson, 1935).

The inheritance of four dominant color factors and the "wild type" in both biparental and parthenogenetic breeding in the species Telmatettix axtecus Saussure was reported by Nabours and Snyder in 1928, and five years later the inheritance of twenty-four dominant color patterns and the "wild type" in the species Acrydium arenosum Burmeister was described by Nabours, Larson, and Hartwig (1933).

Bellamy (1917) reported the inheritance of five color patterns for Tettigidea parvipennis. Many of these patterns are described more fully in the present paper. Since Bellamy's experiments, but one worker has added to the genetics of Tettigidea parvipennis. Morgan (1938) showed that the inheritance of wing length was due to an allelomorphic pair of genes, short wing (S) dominant to long wing (s).

The species Tettigidea parvipennis was first described by Harris in 1835 (Hitchcock, 1835). It is frequently alluded to as Tettigidea lateralis Say by taxonomists; but many synonyms have been proposed. The establishment of the species has been difficult because of the dimorphic condition of the lengths of the wings and pronotum.

The geographical range of Tettigidea parvipennis covers the entire area east of the Rocky Mountains from Central America to Canada and to the Atlantic coast. None has been reported from the west coast.

The habitat is usually moist, rocky creek beds or lake shores, particularly in the late spring and summer (Stehr and Branson, 1938), though the species has been taken in wooded areas. Tettigidea parvipennis and Acrydium arenosum appear to make use of cover and shade more readily than Apotettix curycephalus, Paratettix texanus and Paratettix cucullatus.

Specimens for breeding have been collected from Texas, Louisiana, Mexico, and in the vicinity of Manhattan, Kansas. They are reared in cages and when mature are recorded for color patterns and wing lengths. Many of the recorded specimens have been preserved in 95 percent alcohol and hermetically sealed in glass vials where they are available for further reference.

NOTES ON BREEDING CONDITIONS

Although the experimental breeding was carried on in the regular breeding cages as described by Nabours (1914, 1917, 1923, 1929, 1937), other jars and containers have been tried with

varying degrees of success. The principal disadvantages of the regular glass jars are their large size and cost, yet it has been found that they are the best for maximum hatches of offspring. Screen cages with tin around the bottom to about four inches in height were tried. Although no change in size of cage was made, the numbers of offspring were smaller. Indications are that such cages can be used effectively if a more constant temperature than the ordinary greenhouse daily fluctuations is maintained. Perhaps one of the principal advantages of the glass jars is that the temperature changes less abruptly, though they do attain an undesirably high temperature when in the sunshine. Screen cages also permitted greater changes of humidity and soil desiccation.

Another attempt was made by using a box 14" x 17" x 6" filled with sand and a layer of loam. Quart fruit jars from which the bottoms had been removed were inverted in the soil and covered with screen. In this way space could be saved and the large box would retain moisture longer and more evenly between jars. Since it was too late in the breeding season for Tettigidea, this method was applied only to Apotettix. Some offspring were produced but again not in sufficient numbers to warrant continuing the experiment. The season was late fall and poor breeding was then general even in the regular stock jars.

During the winter months quart fruit jars were tried again. They were set in saucers and a small layer of sand and one of loam placed in the jar. The top was covered with cheese cloth and a nearly constant temperature maintained. Although offspring

did hatch, the numbers were small.

Milk bottles were used with approximately the same results as with the fruit jars. The temperature probably did not fluctuate more than three degrees either way from 26° C. In this case the bottoms of the bottles were not removed and cotton plugs and cheese cloth covers were used, depending on the relative wetness of the soil in the bottle.

The last two experiments were carried on under artificial light. As has been shown by Sabrosky, Larson and Mabours (1933) light is important for winter breeding. Though the experiments of Sabrosky, Larson and Mabours have been criticized by Strohecker (1937), no reliable tests have been conducted to separate the effects of heat and light. However, a reduction in both slows the rate of growth of Tettigidea parvipennis nymphs.

The value derived from these experiments seems to be that any of these types of cages could be used for retaining breeding stock and hence save space and expense. The success of small containers is contingent on the care with which moisture, food, and temperature are controlled.

Although the effect of confinement has not yet been determined, it is thought that with a high quality of maintenance, as many as 15 adult males and 10 adult females could be held in an area no larger than that within a quart fruit jar.

FEEDING EXPERIMENTS

In order to ascertain the food of the grouse locusts, an examination was made of the pool-bottom algae without much of the longer more filamentous algae. The survey showed an abundance of fine filamentous, branched algae as well as flocculent algae of a brownish color. Also present was an abundance of diatoms as well as protozoa, etc.

A sample of this food was fed to the grasshoppers. The digested pellets were caught in a dish of water directly after passing from the grasshoppers through a screen drop board. After lightly mashing the pellets they were examined under the microscope. In the pellets were small fragments of filamentous algae. The cells showed a differential degree of digestion between almost total and that in which the cells were plasmolysed. Cells in which damage to the cell wall could be detected appeared more completely digested than those in which no damage to the wall could be detected. The digestion, in part, was shown by a change in the color of the constituents in the cell. Instead of the bright green color alone, as in the control sample, it was found that the color ranged from green and brown, to brown, and to that in which color was scarcely evident.

The analysis of the excreta showed an absence of the flocculent material mentioned above, unless a brownish material, not flocculent, was the same material in a slightly different form. There was none of the fine, highly branched filaments of algae. These apparently had been digested completely. A very few diatoms remained.

A series of experiments to find, if possible, a substitute food material in place of the known algae foods was undertaken. Table 1 gives the results of the feeding experiments. A "+" indicates that some of the food had been eaten and a "-" that none of it had been taken. Observations were made four times daily and once in the evening. The decision as to edibility of the food was made on the basis of observance (1) of the grasshoppers actually resting on the food (not necessarily eating, except in a few cases) and (2) the number of pellets found in the jar. Most of the grasshoppers were in a condition of near starvation throughout the experiment.

Table 1. Results of feeding experiments.

Bran and yeast (irradiated)	-
Oat mix ($CaCO_3$, oat meal, yeast, evap. milk powder, and syrup)	-
Bran and syrup	-
Bran, oat mix, and yeast	-
Bran, orange juice, and mashed rind	-
Bran and mashed orange rind	-
Bran and mashed onion	+ +
Bran and cod liver oil	-
Bran, cod liver oil, and sugar	+
Ground oat sprouts (12 day)	-
Onion and orange	-
Oat mix and cod liver oil	-
Oat mix, onion, and orange	-
Bran, onion, orange, and yeast	-
Ground elodea and old onion	-
Ground elodea and cod liver oil	-
Ground elodea and sugar soln	-
Ground fern leaves	-
Ground oat shoots and sugar soln	-
Ground tender young water lily leaves	-
Ground onion (old) and orange	+
Ground orange (old)	-
Onion, orange, bran, oat sprouts, elodea, and algae	-
Ground alfalfa (young leaves)	-

NOTES ON THE LIFE HISTORY

Mating of the grouse locusts occurs early in the spring and continues throughout the summer. The male rides about on the larger female for days and apparently copulates continuously. The female becomes, after a time, resigned to the male's presence and goes about feeding, etc., as usual (Hancock, 1902). The male does not require any food for the days he rides about on the female.

A brief survey of the copulation habits of the species in the laboratory revealed that a single copulation period varied from a few hours to as long as four days. An average from 27 matings showed that a pair copulated 6.46 mornings and 8.03 afternoons in a period of 19.67 days between the first and the last copulation though the pairing lasted 26.53 days. The records were made from the middle of May to the first of July.

If the female is in prime condition egg laying commences at once and continues for a short but indefinite period of time. Fifteen to twenty-five eggs are deposited in a cluster in the soil at one time, preferably within or under a clump of algae or other damp humus material. The time from laying to hatching is not definitely known. However, several pairings in which females known to be filled with eggs at the time they were placed with a male produced offspring at the end of 13 days. The young emerge from the egg clusters at approximately the same time and are creamy-white, but after an hour or two their color changes to gray.

No definite count has been made of the number of young that hatch or the percentage of viable eggs. However, the young are transferred to new jars within three weeks after hatching, at which time a count is made. The matings for the year 1940 gave an average of 68.53 offspring per productive mating.

The young nymphs feed and grow rapidly. The molts are at irregular intervals. The male casts his exuvia four times before becoming adult while the female has five molts. Thus, the males mature sooner than the females but not all of the males precede all of the females. The laboratory practice has been to separate the sexes after the first male has become mature. The nymphal period for males is roughly four to six weeks and from five to seven weeks for females in the spring and early summer months. The rate of consumption and amount of food required for male and female nymphs is nearly the same. This is not true, however, of the adults, for after maturity the females are quite noticeably greater eaters than are the males.

After the final ecdysis the wings grow to their determinate length. Morgan (1938) reported a genetic factor b linked with s which caused a grayness in the nymph by which the dimorphic forms could be distinguished. This factor has not been observed in the present study nor are other persons in the laboratory able to detect any color difference. As nymphs the wings are small, flipper-shaped pads. The short wings of the adults are of no apparent value, but in the long winged forms the wings may be, though seldom are, utilized for flying.

INHERITANCE OF WING LENGTH

In the Gryllidae, Lutz (1907) has made observations on long and short wingedness (pronotum not considered) in a breeding experiment with Gryllus sp. He concluded that the length of their wings was not conditioned by heredity, but by the environmental conditions under which the individuals grew to maturity.

Wing length in the species Apotettix eurycephalus Hancock and Paratettix texanus Hancock is also not inherited in a simple Mendelian ratio but is directly attributed to the influence of the season. The long winged forms predominate in the late spring and summer months when the growth rate is much accelerated, while the short winged type are more numerous during the fall and winter.

Contrary to the findings in Paratettix and Apotettix, there is no apparent seasonal influence on the expression of the two genes for wing and pronotal length in Tettigidea parvipennis. This correlation was studied on the basis of the matings involving the crossing of a heterozygote with the double recessives (S/s x s/s, s/s x S/s). These crosses theoretically should not be influenced by the environment to any greater extent within a given period than over the aggregate for the year (see Table 2).

An arbitrary limit has been set to separate the two classes of wing length. There is considerable variation of the two extremes but seldom is there any confusion as to whether a specimen is long or short winged. The tips of the jumping legs have been used as the dividing line.

Although the length of the pronotum usually falls in the same class as the wing length, there are many exceptions. A common feature is short wings with an extended pronotum, though not as long as an ordinary long wing pronotum. Numerous cases of stubby (therefore short) specimens which are tentatively assumed to be genetically long winged are found. These are attributed to faulty nutrition and extremes of temperature.

The case in Tettigidea parvipennis is apparently the first reported in Orthoptera in which the length of the wings is known to be controlled by a single pair of genes.

Table 2 shows that there is no seasonal influence which affects the dimorphic character. The data were calculated on the quarterly basis since this most closely approximates the periods of maximum production of offspring. The last quarter of the year is a period of reproductive dormancy.

The long winged form has been reported to be more abundant than the short winged form in Iowa, Indiana, Texas, and eastern Mexico, while the short winged are more numerous in Ontario, New England, and in the vicinity of Manhattan, Kansas. Hybridization of Texas and Manhattan stocks has been accomplished in laboratory breeding. However, there is one type thought to be Tettigidea lateralis Say which will not crossbreed with the regular stocks.

Matings in which two long winged specimens are used produce only long winged offspring (Table 3). Since the long winged form breeds true without exception, the evidence strongly supports the assumption that long winged is the homozygous recessive form.

Table 2. S/s x s/s (and reciprocal) matings showing the absence of seasonal variation on wing dimorphism.

Period	No. of matings	s/s		S/s		s/s total	S/s total	ratio	S/s s/s
Jan.-Mar.	23	266	234	300	291	500	591	1.18 /	1
Apr.-June	77	476	531	549	563	1007	1112	1.09 /	1
July-Sept.	60	235	216	289	257	451	546	1.20 /	1

S/s = short wing
s/s = long wing

Table 3. Matings of wing types.

Type of mating	No. of matings	s/s		S/s		s/s total	S/s total	ratio	S/s s/s
S/s x s/s	160	977	981	1138	1111	1958	2249	1.14 /	1
S(le?)/s x s/s	33	93	78	321	296	171	617	3.60 /	1
Sle/s x Sle/s	23	118	113	217	225	231	442	1.90 /	1
s/s x s/s	34	323	317			650			

le = lethal

The mating of two heterozygous short winged specimens should produce a 3 : 1 ratio. Although the data are not exactly 3 : 1 in Table 3, by statistical treatment the difference is shown to be not significant.

The majority of matings were of the heterozygous short winged and long winged crosses. These data should present a 1 : 1 ratio. However, a slight excess of short winged offspring is shown. When the data are handled statistically the difference in the ratios is found to be significant. As shown in the tables the number of short winged specimens mated exceeds the long winged parents by 84. In many cases specimens for mating were selected before a permanent record of the group was made, the short winged type having been mated more often than the long winged, while many of the long winged form undoubtedly perished before any record had been made. Even this slight correction is nearly enough to make the difference statistically non-significant.

The work of Morgan suggested a lethal linked with short wing in part of the stock. There was a deviation in the progeny from one Manhattan specimen from approximately the 3 : 1 ratio to a ratio approaching 2 : 1, the short winged form still more numerous. A pedigree chart showing quite conclusively the presence of this lethal has been worked out, and the numerical data conform with the pedigree in support of the theory of a linked lethal designated Sle.[1] In one instance the lethal crossed out or became non-active in succeeding generations. Inbred stock

[1] Unpublished data.

from Texas does not show the presence of the lethal.

The study by Morgan (1938) of the relative difference between the long and short wings gave the following measurements from 300 specimens of each type.

Table 4. Measurements of long and short wing specimens.

	Males		Females	
	wings	pronotum	wings	pronotum
Long	2.88 mm.	.976 mm.	2.75 mm.	.99 mm.
Short	-1.94 mm.	-.975 mm.	-1.93 mm.	-.99 mm.

(from tip of femora to posterior point of wing or pronotum)
(-) = anterior to femora tips

It can be seen from the data of Table 4 that in general the length of the pronotum corresponds to the length of the wings although this is not true in every case.

Table 5 gives the numerical basis for the grouping of the factors on the different chromosomes. These data are further strengthened by more recent figures and numerous observations. The percentage of crossing over is determined in the F_1 generation by the number of offspring that are not of the two parental phenotypes (with respect to the characters in question). When the parental combinations considerably exceed the new (non-parental) combinations the new combinations are considered to be crossovers. If the new combinations equal the parental combinations, independent assortment is suspected, unless it seems reasonable to assume crossing over close to 50 percent. Two factors on opposite chromosomes of a pair will not give any offspring with the parental combinations. If complete linkage is the case all of the offspring should be of the parental

combinations for the characters under consideration. Table 5 does not include all of the patterns described in a later section because no data were then available.

Table 5. Recovery of parental combinations (A) and new combinations (B) in the F_1 offspring.

Factors		(A)	(B)	Factors		(A)	(B)
K	F	74 -	1168	R	K	698 -	730
K	Q	0 -	113	R	F	813 -	886
K	O	0 -	12	R	Q	109 -	142
K	V	0 -	152	R	O	67 -	61
K	Ve	0 -	183	R	V	42 -	34
K	Vd	0 -	34	R	Ve	174 -	142
F	Q	0 -	304	R	Vd	29 -	19
F	O	0 -	297	---	---	---	---
F	V	0 -	255	S	s	690 -	648
F	Ve	0 -	360	S	K	567 -	637
Q	V	0 -	9	S	F	854 -	802
Q	Vd	0 -	11	S	Q	93 -	100
O	V	0 -	195	S	O	145 -	159
O	Ve	0 -	37	S	V	48 -	44
---	---	---	---	S	Ve	38 -	44
CS	K	109 -	106	S	R	465 -	459
CS	F	208 -	253	S	C	349 -	0
CS	Q	73 -	69				
CS	O	16 -	10				
CS	Ve	5 -	5				
CS	R	214 -	172				

PATTERN FACTORS

The patterns studied are as follows (in their respective chromosomal groups):

+/+ - "wild type", a grayish-black color with a crisscross marking; acts as a complement to other color patterns in completing Mendelian ratios.

K - narrow stripe along carina of pronotum devoid of black pigment from head to posterior tip; dominant.

Q - buff color over all of the pronotum and crown of head, incompletely obscures +/+; dominant.

O - creamy white over all of the pronotum and crown of head; dominant.

U - mottled buff less completely obscuring +/+ than Q; dominant.

V - veining of the pronotum, conspicuous in male, barely (if at all) recognizable in female; dominant in male.

Ve - strong white veining of pronotum in male and female; dominant.

Vd - white veining of pronotum with dark non-veined area along carina and heavy white stripes along edges of femora of jumping legs; dominant.

Vs - white veining of the pronotum with a reduced stripe on femora of jumping legs; dominant.

F - white spot on dorsolateral area of hind legs; dominant.

Tm - black-tipped red cuffing on distal half of posterior

legs, white spot at anterior edge of cuff and a whitish mottled pronotum; dominant.

These patterns are apparently located on one pair of chromosomes (Table 5). No crossing over is known. It could be assumed that at least three loci are involved with several allelomorphs at each; K,Q,O,U, at one; F, at another; V,Ve,Vd, Vs, at a third and the Tm probably a combination of several loci.

The veining of the pronotum is due to ridges on the pronotum on which the pigmentation is light colored and contrasts with the background. The simplest veining is Ve which produces the veined condition equally in males and females. It is an ordinary autosomal character. Vd and Vs are easily distinguished from Ve by accessory patterns on the femora of the back legs, and other pronotal characters.

The most unusual of the veined patterns is V. Its sexually dimorphic expression is not yet quite clear. It is certain that in the male the factor shows clearly if present, except when obscured by other patterns. In the female it is hardly expressed but is transmitted by them to the succeeding generation where it shows in the males.

The character acts as though it were sex limited but as yet individuals homozygous for V have not been obtained. Cases of true sex limitation are not common except as secondary expressions of sex. From the sexual standpoint there appears to be no reason for the sexes to differ in their expression of V. Though it may be questioned as to whether V

should be classed as a sex limited character there is no question about its being sexually dimorphic.

R - red color on the pronotum and distal tips of femora of jumping legs, several variations; dominant.

Ch - chocolate color occupying same area as R; dominant.

The R and Ch are probably on the same pair of chromosomes (Table 5).

S - short wing, associated with a short pronotum - many exceptions; dominant to s - long wing, usually a long pronotum; recessive to S.

C - red cuffing of the femora of jumping legs linked with short wing; dominant.

le - lethal linked with S; recessive.

These three factors are on a third pair of chromosomes (Table 5), the first factor with its allele constituting a strictly Mendelain pair. The lethal was lost before the present investigation began.

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yl - yellow color over entire body and legs; recessive (?).

Cr - red cuffing of the psterior femora together with a red colored pronotum; dominant.

re - red eyes with a yellowish cream pronotum; recessive.

These are as yet not located.

The various cuffings (C,Cr,Tm) are each located on different pairs of chromosomes. Each of them is distinguished

by an accessory marking, since the red part of the cuffing itself is quite similar in each case. This evidence points to the conclusion that at least three of the six pairs of autosomes are concerned with the pigmentation of the femora of the jumping legs. These patterns are the only ones with which linkage might be justly claimed. In each the linkage is complete and no known segregation has been recorded of the cuffing separate from its accessory pattern. Tm and Cr were brought in from near Houston, Texas, and C from around Manhattan, Kansas. Neither of the Texas types has so far been collected in the Kansas region nor has the Kansas type been found in Texas.

SUMMARY

1. Brief sketches are given of the habitat, copulation habits, numbers of eggs per cluster, average number of offspring per mating, instars and feeding habits of the grouse locust, Tettigidea parvipennis Harris.

2. The results of several experiments with different kinds of cages showed that smaller cages can be used if a higher quality of maintenance is practiced.

3. An effort to produce a synthetic food to replace the regular algae feeds was unsuccessful. However, it is shown that the algae which are fed furnish the nutriment necessary for growth of the grasshoppers.

4. An analysis of a lethal factor in the older records is substantiated although no specimens were available for breeding proof.

5. Additional data more conclusively show that the dimorphic wing condition is due to a pair of allelic genes which is not affected by the season.

6. Nineteen factors are reported for the species Tettigidea parvipennis. Of these, ten are located on one pair of autosomes, three on another, two on a third, and three as yet not located, and the wild type.

(1) K,Q,O,U; V,Ve,Vd,Vs; F; Tm

(2) C, S, le

(3) R, Ch

(?) Cr, re, yl

For reference, Bellamy's (1917) characters are here presented with their present equivalent:

Bellamy		Good
C	=	K
E	=	Vd
F	=	F
H	=	R
D	=	No specimens

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