INHERITANCE OF SOME MORPHOLOGICAL CHARACTERISTICS IN THE GROUSE LOCUSTS (*APOTETTIX EURYCEPHALUS* HANCOCK)

by

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INTRODUCTION

Considerable study has been made of the inheritance of the color patterns of several species of the grouse locusts of the sub-family Tetriginae, by Doctor Robert K. Nabours and his students, but very little attention has been given to the inheritance of structural characteristics as length of wings and pronotum, and various abnormalities such as twisted pronotum, club-wings, or abnormal abdomen which are of fairly common occurrence.

The purpose of the research herein reported was to collect data to determine if morphological variations as wing length, twisted or arched pronotum, stubbiness, fused sterna of the abdomen, and frayed or crossed wings, were inherited, or merely expressions of environmental influence.

REVIEW OF LITERATURE

It has been suggested by Nabours (1914) that the condition of long-wingedness or short-wingedness was not determined by discrete hereditary factors, but by the environmental influence coincident with the time of the year during which growth occurred. The short-winged forms predominate to a great extent in the late fall and winter when growth is slow, and the long-winged forms predominate in the spring and summer when development is more rapid. Lutz (1907) concluded that the length of wings of the species of Gryllus with which he carried on experiments, was not determined by heredity, but by the environmental factors under which the individuals grew to maturity.

Some of the abnormalities described in *Drosophila melanogaster* are similar to those found in the grouse locusts. Bridges and Morgan (1919) reported on a recessive factor causing a wing abnormality "antlered", in which the wings form right angles with each other, the tips being bent sharply posteriorly. Quelprud (1931) has reported on a second chromosome wing mutant which causes a condition similar to "antlered". Ward (1923) discussed the factor for "curly" which causes the wings to curl upward and forward. This factor is dominant, and is lethal in the homozygous condition.

The abnormality "ski-wings" reported by Clausen and Collins (1922) in Drosophila depends for its appearance upon the action of a dominant gene on chromosome II, and a recessive gene on chromosome III. Neither of these genes produces any visible effect in the absence of the other; together they regularly produce the ski-wing character. The second chromosome dominant intensifies the ski characteristic when it is homozygous, but is sufficient in heterozygous condition to produce a definite and easily separable character.

Komai (1926) discovered a recessive, "crippled", which is modified by the environment, sometimes concealed even in the homozygous state. The factor causes the segments of the legs to be shortened, broadened, crooked, fused, twisted, or entirely missing. Richards (1929) found in ten stocks which had been treated to reduced temperatures, two new mutations, blistered wings and abnormal abdomen. These two inherited characters appeared frequently among the progeny of "iced flies".

Morgan and Bridges (1916) reported on a dominant factor "abnormal abdomen" in Drosophila melanogaster, which is very similar to one found in the grouse locusts. This factor, which produces fusion of the sterna of the abdomen, is strongly influenced by the environment. It is most marked in flies reared under moist conditions and may be suppressed entirely under dry conditions. However, rearing the stock for several generations under dry conditions, did not decrease the intensity of the character in the offspring when the same lines were later reared under moist conditions.

Sturtevant (1929) describes two recessive factors in *Drosophila simulans*, abnormal wings and curved wings, in which the wings are held at right angles to the body and curved downward. Stocks carrying these two factors have poor viability.

Umeya (1930) reported on the inheritance of abnormal genitalia and the effect of the environment in the male moth of *Bombyx mori* L. In a pure breed of Japanese silkworms, males with abnormal genitalia occasionally appeared. Experiments were conducted to determine the incidence of this abnormality in progeny of such males mated to normal females, the progeny being exposed to different temperatures at various stages of development. Exposure to high temperatures (27-30° C.) during pupation, yielded the highest proportion of abnormal males.

Whiting (1926) reported on two recessive traits, wrinkled and reduced wings, in one of the wasps, Habrobracon. "Wrinkled" prevents normal expansion of wings, and "reduced" causes the wings to be much shortened and the veins to be reduced or fused.

MATERIAL AND METHODS

The grouse locusts, Apotettix eurycephalus Hancock, used in these experiments belong to the southern species of the sub-family Tetriginae. Members of this sub-family are distinguished from other grasshoppers by the development of the pronotum which extends backward over the mesonotum and metanotum. They are usually dimorphic in that the wings and pronota may extend either to the distal ends of the femora of the jumping legs, or beyong that point. The stocks used in these experiments were originally collected in southern Mexico and southern Texas.

Members of the species, A. eurycephalus produce four generations a year in the greenhouse. A pair of mature individuals were placed in each mating jar, and allowed to remain together until the female died. Dead parents were preserved in alcohol. The jars were examined daily for the appearance of offspring. Soon after emerging from the ground, where the eggs were deposited, the young were transferred to other cages in which to attain the imago. The offspring cages were examined three times a week, and all adults, except those reserved for further matings, were preserved in alcohol. The parthenogenetic females and their offspring were treated in the same manner.

The cages used were Pyrex glass cylinders, about eight inches in diameter and twelve inches in height, set in bulb pots filled with sterilized sand and loam at the bottom and top, respectively. A three or four inch pot, with the hole plugged, was inverted over the hole in the bulb pot before the sand and loam were put in. This inside pot was to provide for better aeration of the soil, and to hold the food, which was mainly filamentous algae. The cylinders had covers of 24-mesh screen wire (Nabours, 1929).

Records were kept of the color patterns and morphological features of both the parents and the offspring. The number of offspring and the period of time required for them to become adult were also noted. In most cases, the offspring were allowed to reach the imago, as no data on the various characteristics studied, could be obtained until then.

Besides the data obtained during the past year, much has been taken from the many records kept by Doctor Nabours over a period of more than twenty years.

EXPERIMENTAL DATA

The first characteristic to be considered is that relating to the length of wings and pronota. The grouse locusts may be either long-winged or short-winged. In the long-winged forms, the pronotum extends a few millimeters beyond the tip of the abdomen and the distal ends of the femora of the jumping legs, and the wings usually extend two or three millimeters further. In the short-winged forms, the wings and pronota extend just to the tip of the abdomen and the distal ends of the femora of the jumping legs. There are also occasional intermediate types. Both in the greenhouse and in nature, the long-winged forms predominate in the spring and summer, whereas the short-winged ones predominate in the late fall and winter, as shown by the many records of those reared in the greenhouse, and by field studies.

Two parthenogenetic lines have been studied in detail as to length of wings and pronota. These have been selected because they should breed true for all factors, even from the second generation. Their prolificness is much reduced from that of mated females.

Tables I and II illustrate long and short-wingedness in these two parthenogenetic lines. The first column in each

Table I. Wing Length in Parthenogenetic Line A.

Generation	Period of Growth	No. of long wings	No. of short wings	Total	Percent long wings	Percent short wings
1	Apr. to May	32	4	36	88.8	11.2
2	June to July	18	1	19	94.7	5.3
3	Sept. to Nov.	4	6	10	40.0	60.0
4	Jan. to Apr.	0	15	15	0	100.0
5	May to Aug.	17	4	21	80.9	19.1
6	Nov. to Feb.	1	3	4	25.0	75.0
7	Mar. to June	1	2	3	33.4	66.6
Totals:		73	35	108	67.6	32.4

Table II. Wing Length in Parthenogenetic Line B.

Generation	Period of Growth	No. of long wings	No. of short wings	Total	Percent long wings	Percent short wings
1	July to Sept.	11	0	11	100.0	0
2	Nov. to Feb.	7	11	18	38.9	61.1
3	Mar. to July	19	5	24	79.2	20.8
4	July to Sept.	19	6	25	76.0	24.0
5	Oct. to Jan.	0	7	7	0	100.0
6	Mar. to May	2	8	10	20.0	80.0
7	May to July	5	2	7	71.4	28.6
8	Sept. to Apr.	0	15	15	0	100.0
Totals:		63	54	117	53.8	46.2

table gives the number of the generation; the second column, the approximate period of growth; the third column, the number of long-winged individuals; the fourth, the number of short-winged individuals; the fifth, the total number of off-spring; the sixth, the percentage of long-winged; and the seventh, the percentage of short-winged in the generation. The totals for the entire line are given at the bottom of the tables.

Parthenogenetic line A, given in Table I, continued for seven generations, and produced 108 offspring, 73 or 67.6 per cent of which were long-winged, and 35 or 32.4 per cent of which were short-winged. There were more long-winged than short-winged individuals in the totals, because the short-winged usually grew during the unfavorable part of the year when mortality was high. Of those in which growth occurred from March to September, 88.2 per cent were long-winged, and 11.8 per cent were short-winged, but those which grew during the period from November to March, 18.7 per cent were long-winged, and 81.3 per cent were short-winged. From a single generation, such as the fourth, the offspring, which had a growth period extending from January to April, were all short-winged. In contrast, the second generation, in which the growth period was from June to July, 94.7 per cent were long-winged, and 5.3 per cent were short-winged.

In Table II, parthenogenetic line B is illustrated. There are nine generations, of which the last is not yet adult. From this line there were 117 offspring, of which 63 or 53.8 per cent were long-winged and 54 or 46.2 per cent were short-winged. Of those that grew from March to September, 80.7 per cent were long-winged, and 19.3 per cent were short-winged, while of those that grew from September to March, 18 per cent were long-winged, and 82 per cent were short-winged. In the first generation, in which growth occurred from late July to September, all were long-winged. In the eighth generation, which grew from September to April, all offspring were short-winged. There is, therefore, a close correlation between the percentage of long-winged or short-winged, and the period during which growth occurs.

"Abnormal abdomen" is a condition in which the sterna of the abdomen are fused or present only in part. The sternum may be almost entirely missing so that it gives the appearance of an extra piece. This abnormality was found in a parthenogenetic line of grasshoppers which continued for six generations. This family is illustrated in Chart I. The normal parents and offspring are denoted by the symbol "n"; those which showed the abnormality are denoted by the symbol "abn". Each bracket represents a generation; the months above represent the period during which growth occurred. There were 217 offspring in this line, of which 151 or 69.5 per cent were normal, and 66 or 30.5 per cent were abnormal. The conditions under which they grow probably also influence the appearance of this character.

A third characteristic studied has been designated as "stubby". The pronotum of a stubby adult is blunt and short, and does not taper to a normal point. It resembles somewhat the pronotum of a nymph. The wings are wrinkled, short, reduced, or otherwise deformed. The term "stubby" covers a number of pronotal abnormalities, ranging from a blunt pronotum and extremely short wings, to slightly pointed pronotum and slightly deformed wings. This characteristic has continued for a number of generations in a group of closely related individuals.

Much difficulty is encountered in rearing these stubby animals to the adult stage. Only a small proportion of those hatched reach the imago, and then only after a comparatively long period, often extending over several months. For example, a mating between a stubby male and a normal female produced twenty-two offspring, that required from October 20 to February 6 to become adult. In another case, two stubby animals produced seventy-two offspring that required from March 8 to June 12. Normal offspring, in contrast, require only about six to eight weeks during the

Chart I. Inheritance Chart of Abnormal Abdomen.

- n
  - Mar. to June
    - 71 n
    - 9 abn
      - June to Sept.
        - 23 n
          - Sept. to Oct.
            - 1 n
            - 0 abn
        - 41 abn
          - Sept. to Nov.
            - 1 n
              - June to Aug.
                - 3 n
                - 2 abn
                  - Apr. to June
                    - 31 n
                    - 0 abn
            - 4 abn
              - Nov. to Mar.
                - 2 n
                - 5 abn
                  - Apr. to June
                    - 6 n
                      - July to Aug.
                        - 1 n
                        - 0 abn
                      - Dec. to Mar.
                        - 3 n
                        - 2 abn
                    - 0 abn
              - Dec. to Mar.
                - 7 n
                - 1 abn
                  - May to July
                    - 2 n
                    - 2 abn

same season, to attain the imago. As in other morphological abnormalities, stubbiness cannot be detected until the adult stage. Attempts have been made to recognize "stubby" in the third and fourth instars, by separating those which appeared stubby from those which did not, but the results were not satisfactory.

Experiments have been conducted to test the possibility of hastening the rate of growth by rearing the stubby stock under continuous violet-light from a Cooper-Hewitt mercury vapor lamp. Jars containing equal numbers of offspring from the same matings were divided into two groups. Some were placed under the violet light, and some were kept under ordinary greenhouse conditions to serve as the controls. Those under the violet light grew more rapidly at first, and reached the fourth instar six to ten days before the controls. From then on, however, their growth was very slow so that both groups matured at approximately the same time. The light apparently did not affect the proportion of stubby ones obtained.

The entire line of stubby animals is given in Chart II. A normal animal is denoted by the symbol "n"; one showing the stubby characteristic, by the symbol "s". The matings are indicated as s x n, n x n, etc. The first number under the mating indicates the total number of offspring that became adult; the number in parentheses indicates the number of stubby offspring. For example, $\overset{n \times s}{11\ (2)}$ means a normal male was mated to a stubby female, and produced eleven offspring, two of which were stubby. The months below the number of offspring represent the period of growth.

"Upturned pronotum" was another abnormality studied. This factor causes the tip of the pronotum to be sharply upturned, so that it is at a distinct angle with the main plane of the pronotum. This characteristic was first observed in the fall of 1932. Four females, offspring of the original normal pair, produced parthenogenetically eleven offspring, three of which had upturned pronota. Only one mating in which one of these parthenogenetic females was mated to a normal male from the same line, has any offspring which are adult. Of these sixty-five adult offspring, two males show the abnormality. Two of the original eleven offspring reproduced parthenogenetically. These females showed this condition of upturned pronota, and all eight of their offspring show the same abnormal condition. This line can be shown in a short chart, in which "n" denotes the normal, and "upt", the abnormal condition. As in Chart II, the first number represents the total offspring that became adult, and the number in parentheses, those offspring that showed the abnormality. The months above represent the

Chart II. Inheritance Chart of Stubbiness.

- n x n 17(0) Aug. to Sept.
  - n x n 12(5) Feb. to May
    - n x n 31(4) July to Aug.
      - n x s 5(0) Nov. to Feb.
      - n x n 11(0) Nov. to Jan.
    - s x n 1(0) July to Aug.
    - s x s 9(3) July to Aug.
      - n x n 13(0) Oct. to Jan.
        - n x n 4(0) Feb. to Mar.
        - n x n 62(3) Feb. to May
          - n x s 6 (0) May to July
          - n x s 5(1) May to Aug
            - n x n 4(0) Nov. to Mar.
            - n x n 3(3) Oct. to Feb.
            - n x n 14(0) Sept. to Nov.
        - n x n 1(0) Mar. to June
        - n x n 46(4) Mar. to June
          - n x s 6(3) June to Oct.
            - n x s 9(4) Oct. to Feb.
        - n x n 31(2) Mar. to May
          - n x n 1(0) May to Aug.
      - n x n 15(2) Sept. to Jan.
        - n x n 14(0) Mar. to May
        - s x s 59(4) Mar. to May
          - n x n 5(0) May to Aug.
            - n x n 2(2) July to Nov.
          - s x s 1(0) June to July
          - s x s 4(0) May to Aug.
        - n x n 9(0) Feb. to Apr.
          - s x n 2(0) May to July
          - s x n 3(0) May to Sept.
            - n x s 22(15) Oct. to Jan.
          - n x s 2(2) May to Sept.
      - n x n 12(1) Oct. to Dec.
        - n x s 11(2) Feb. to May
          - n x n 3(2) June to Sept.
      - n x s 5(1) Oct. to Dec.
        - n x n 25(1) Mar. to May
        - n x n 23(0) Mar. to May
          - n x n 6(0) May to Aug.
            - n ♀ 3(3) Sept. to Feb.
        - n x s 38(1) Feb. to Apr.
    - s x s 1(1) July to Aug.
    - s x n 6(3) July to Aug.
      - n x n 14(2) Nov. to Jan.
        - n x s 5(0) Mar. to May
        - n x s 18(2) Feb. to May
          - s x s 1(1) June to Aug.
        - n x n 56(5) Mar. to May
        - n x n 21(0) Feb. to Apr.
          - n x n 3(0) May to Aug.
            - n x n 1(0) Oct. to Jan.
      - n x s 6(2) Nov. to Dec.
        - n x s 20(4) Mar. to May
          - n x n 10(0) May to July
            - n x n 25(0) Dec. to Feb.
            - n x n 7(1) Dec. to Feb.
            - n x n 12(0) Oct. to Feb.
            - n x n 3(0) Oct. to Feb.
      - n x s 2(1) Nov. to Jan.
        - n x s 9(0) Mar. to Apr.
          - n x n 2(0) June to Sept.
            - n x n 20(0) Nov. to May

periods during which growth occurred.

May to June n x n 11(0)	Nov. to Jan. n ♀ 5(0)	
	Feb. to Apr. n ♀ 1(1)	May to June upt ♀ 4(4)
	Nov. to Jan. n ♀ 2(2)	May to June upt ♀ 4(4)
	Oct. to Dec. n ♀ 3(0)	Mar. to June n x n 65(2)

The female that showed the abnormality "club-wings" was also found in 1932. She had a rather short pronotum, and wings which curved out from the body at an angle, and gave the appearance of hockey clubs. She produced, parthenogenetically, eighteen offspring. Only five of these became adult, two of which showed the same abnormality as the parent. This line has not produced any more offspring.

Several other abnormalities are found in this species of grouse locusts. Some of the more common ones are: "twisted pronotum", in which the tip is sharply twisted to one side; "arched pronotum", in which the tip is arched up; "downturned pronotum", in which the tip of the pronotum is sharply turned downward; "frayed wings" in which the posterior parts are wrinkled or shiriveled; and "crossed wings", in which the tips are crossed over each other. As yet, no discrete factors have been determined for them.

DISCUSSION OF DATA

The records of the matings and parthenogenetic females show that the long-winged forms predominate in the spring and summer when growth is rapid, and the short-winged ones predominate in the late fall and winter when growth is slow.

There appears to be no definite inheritance of long-wingedness or short-wingedness, but a tendency to inherit the capacity of being either long-winged or short-winged, dependent upon the season during which they grow. One would expect the second generation of parthenogenetic grouse locusts to be homozygous for all factors. However, in each generation, even to the seventh and eighth, of the parthenogenetic lines herein reported, both long- and short-winged individuals occur. Therefore, there are probably no discrete factors for the various lengths of wings and pronota, but the length depends on the influence of the environment during the season of growth.

Fusion of the sterna of the abdomen, termed "abnormal abdomen" was found in a parthenogenetic line which continued for six generations. The fact that this abnormality continued through so many generations in one line and in no others indicates the presence of distinct genetic factors. However, it does not behave either as a simple recessive or dominant unless it is influenced by modifying factors. This factor may be inherited recessively because, of the few outcrosses made from this line, there have been few abnormal abdomens found in the subsequent offspring. In the entire line there are 113 normal and 11 abnormal offspring from those females that were normal, and 44 normal and 55 abnormal from those females that were abnormal. The numbers in this case are few, but significant. Further work on this factor may determine its linkage relations.

The inheritance of stubbiness is very complicated. Although it appears consistently and only in one line, it has not been assigned to a single factor or located on the chromosome map because of the aberrant Mendelian ratios. Whether it is a dominant or a recessive, has not been determined since normal parents can produce stubby offspring and vice versa. Its expression is modified by seasonal conditions as there are many more stubby ones during the season of slow growth, that is, late fall and winter, than there are during the season of rapid growth, spring and summer. For example, the offspring of one mating became adult during January and February, and twenty-three out of thirty offspring were stubby. A mating was made from two of these stubby progeny. Their offspring became adult during May and June, and none was stubby. The expression of this factor is so modified by the favorable growing conditions of the spring and summer, that no stubby animals may appear, though some, or all, of them must carry the genes for stubbiness.

The factor for upturned pronotum behaves as a recessive. The original mating was a normal x a normal. Three of the eleven offspring showed the abnormality. The two abnormal females which have produced parthenogenetically, produced eight offspring, all of which had upturned pronota. The other abnormal female was mated to a normal male of the same line. From this mating there are sixty-five adult offspring, two of which have upturned pronota.

As yet we have not been able to determine if special factors exist for the twisted, arched, or downturned pronotum, and frayed, crossed or club-wings. They may be different manifestations of one factor, conditioned by various environments.

SUMMARY

1. The grouse locusts, *Apotettix eurycephalus* Hancock, inherit the capacity or ability to be either long-winged or short-winged, depending on the environmental conditions of the season during which growth occurs.

2. Fusion of the sterna of the abdomen is inherited perhaps as a recessive factor greatly modified by the environment.

3. Stubbiness is inherited, though it is not yet determined whether as a recessive or a dominant.

4. "Upturned pronotum" is inherited, probably as a recessive.

5. Special factors apparently exist for twisted, arched, and downturned pronotum, frayed, crossed, and club-wings, respectively.

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