THE GENETICS OF THREE LARVAL COLOR FORMS IN *CHLOSYNE LACINIA* AND THE PHENOTYPIC FREQUENCIES OF THIS POLYMORPHISM IN NATURAL POPULATIONS

by

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ABSTRACT

Three larval color forms of the nymphalid butterfly Chlosyne lacinia (Geyer) occur in natural populations. Nigra is the black form, bicolor differs from nigra in having a mid-dorsal orange band extending the length of the body, and rufa is the orange form. The genetics of these forms and also their phenotypic frequencies in natural Arizona populations of the Mesa-Chandler-Higley are were studied.

Larval progenies were fed sunflower plants (Helianthus annuus Linnaeus), and reared in the field or in the laboratory. Adults were fed sugar water from a sponge. Mating was accomplished in one of two ways: adults were either allowed to mate on their own, or were aided by a modified hand-pairing technique.

The progeny data suggest that the genetic mechanism is a non-linked, two locus, epistatic system. The bicolor and rufa determining alleles are dominant over their recessive homologues with the dominant rufa allele epistatic over the bicolor locus.

From the phenotypic frequency study of natural populations, a high degree of spacial and temporal heterogeneity was indicated. Three factors were postulated to have contributed to the observed heterogeneity:

a) the fecundity effect, or the large number of offspring that

one female can contribute to a population,

b) the progeny effect, or the large number of offspring in a colony coupled with their gregarious habit, and

c) the neighborhood effect, or limited intergeneration dispersal of adults.

The fecundity effect is not an inherent error of the sampling procedure but is a phenomenon of small populations. The progeny effect is related to the problem of obtaining a random sample of offspring from various matings.

During the study it was observed that the phenotype frequencies differed between two years at one locality. It was proposed that yearly phenotype frequency changes were caused by a phenomenon similar to the founder principle. Because of the spring drop in population size, frequencies may change due to gene frequency changes resulting from the population's sampling error.

It appears that populations generally tend to maintain each phenotype at a characteristic frequency. The pooled data from the Mesa-Chandler-Higley area produced the following phenotype frequency estimates (relative to each locus) for the year 1969: rufa, 0.188; non-rufa, 0.812; bicolor, 0.811; nigra, 0.189.

The phenotype frequency data from two years, at a single locality, suggest temporal stability. An interesting frequency observation from the pooled data was made. Relative to a single locus, the rufa and nigra larval types occur at approximately the same frequency, thus suggesting an interaction of genotypes.

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INTRODUCTION

The objectives of this study were to determine the genetic mechanism of the three polymorphic larval color forms of Chlosyne lacinia (Geyer) and to observe their phenotypic frequencies in natural populations.

In the Lepidoptera, or other insects with complete metamorphosis, the larval and adult stages are generally under independent genetic control, i.e., a gene responsible for a larval trait is not necessarily responsible for a similar one in the adult stage. This is to be expected since both stages are adjusted to different ecological conditions (Ford, 1953). Genes generally have multiple effects and are integrated into the gene complex that interacts with the environment. Therefore, it would be unreasonable to expect genes to commonly have an adaptive value in both stages of the life cycle and still have the integrity of the larval and adult stage maintained.

The independent genetic control of larval and adult pigmentation is illustrated in the moths Meganephria oxyacanthae Linnaeus, Selenia bilunaria Esper., and Abraxas grossulariata Linnaeus. Melanic larvae of these moths metamorphose into nonmelanic adults even though adult melanic forms are known (Ford, 1953). In Lymantria monacha Linnaeus the melanic larval form is under the control of a single dominant whereas the inheritance of the melanic adult is multifactorial (polygenic) (Ford, 1937). However, an exception occurs in Lasiocampa quercus Linnaeus and Ephestia kuehniella Zell., the flour moth. In

the former the recessive gene that produces the adult variety olivaceo-faciata Cockerell also causes the normal red fur of the larva to be similarly affected (Ford, 1937). A recessive mutant has been found in Ephestia that converts the normal brown eyed adult and brown larva to a pink eyed adult and almost colorless larva (Dowdeswell, 1960, p. 17).

In Lepidoptera two types of polymorphism exist; balanced and transient, the spread of industrial melanism falling into the latter category. Balanced polymorphism differs from the transient type by being stable through time and, therefore, requiring some maintenance factor, or factors, for its continued existence.

An example of balanced polymorphism is the existence of Batesian mimics among the females of Papilio dardanus Brown, a butterfly distributed in Africa (Wickler, 1968, pp. 22-33). Potential maintenance factors, and examples, of balanced polymorphism are: dis-assortative mating in the moth Panaxia dominula L., (Sheppard, 1952); the selective predation by a hymenopteran parasite, Apanteles tetricus Reinhard on the larvae of the butterfly Maniola jurtina Linnaeus, (Ford, 1964, p. 50); and differential flying habit as exhibited in the two dimorphic female forms of Colias eurytheme Boisduval with respect to flying period during a day (Hovanitz, 1948).

However, observed color phases of some butterflies may be incidental expressions of more basic metabolic processes (Hovanitz, 1944). An example occurs in Colias chrysotheme Stephens with respect to two dimorphic adult female color forms that are controlled by a

single locus. On the average, due to a faster developmental rate, the pale form appears in advance of the orange form of each brood (Ford, 1953).

Ford (1953), in a starvation experiment on larvae of Cleora repandata Linnaeus, demonstrated the physiological superiority of melanic dominants. In that experiment larvae that metamorphosed to melanic adults had a reduced death rate even though they themselves were normally colored. Melanics that are less viable than the normal form, as in S. bilunaria and Ectropis bistortata Goeze, have never become established as industrial melanics and exist as rare recessives. As a result, Ford (1953) postulated that the spread of industrial melanism is not a simple matter of cryptic coloration but also involves the greater hardiness of these forms.

In the past the majority of genetic studies of the Lepidoptera have been focused on adult wing color variations. Little is known of larval genetics, but, from what has been done, the inheritance of discrete color traits has been shown to be usually under the control of a single locus.

Gerould in 1921 reported a recessive autosomal mutation in the butterfly Colias philodice Godart affecting blood color in such a manner that the normal grass-green shade of the larval, pupal, and adult eye color was changed to a blue-green shade. In 1926 he reported another blood color mutant, of the same type, that changed the coloration of the above stages to an olive-green shade.

Clarke, Dickson, and Sheppard (1963), working on the genetics

of the umbellifer and citrus larval types of Papilio demodocus Esper, have found the two patterns to be under the control of a single pair of alleles with the umbellifer form dominant or semi-dominant.

In the following moths, the larval phenotypes are controlled by a single locus: the striped pattern of Tropaea luna (Linnaeus), (Wickwire, 1937); the presence or absence of a black dorsal stripe in Lymantria dispar Linnaeus, (Ford, 1937); the albinistic variety and black form of A. grossulariata, (Poulton, 1927; Ford, 1937); and the black larval forms of M. oxyacanthae and S. bilunaria, (Ford, 1937).

BIONOMICS AND LIFE HISTORY

Chlosyne lacinia (Geyer), the patched butterfly, is a nymphalid ranging from the Southwestern United States to Argentina (Ehrlich & Ehrlich, 1961, p. 140). The insect is multibrooded and preferably feeds on sunflower (Helianthus annuus L.), although a high population has been observed on cocklebur (Xanthium saccharatum Wallr.) in an area lacking sunflower. Bush (1969) reports Ximenesia encelioides Cav. as another food plant. C. lacinia prefers mesophilic environments and high populations are usually found on sunflower growing near irrigation ditch banks. Cocklebur is mesophilic and also grows in areas near water.

C. lacinia passes through winter as aggregations of diapausing larvae in dried and curled sunflower leaves still attached to the plant. A silk mat is spun over the leaf surface and any openings, creating an enclosed chamber, possibly serving for protection against spiders, myrmeleontids (antlions), tenebrionids, or other potential predators.

The larvae molt into and out of diapause. The characteristics of the diapausing larva, as compared to the normal feeding form, are as follows: movement is more sluggish (slower), the body coloration is lighter, the spines are tan rather than black, the larval markings appear to be more distinct, and the body surface has a sheen to it. The cast skin, from a caterpillar molting out of diapause, preserves the larval shape in contrast to the shriveled skin of normal molts.

According to Patton (1963, p. 184), photoperiod and temperature are the two principal factors stimulating diapause in insects, with photoperiod the one most likely triggering its onset. Lees (1955, p. 3) states that the termination of diapause in the majority of insects is controlled by temperature, and this is probably the factor influencing C. lacinia since the larvae are hidden from sunlight.

The larvae enter diapause after reaching the penultimate instar, although a few may do so in the last, or 5th, instar. The larval populations sampled from the areas studied (Figure 2) during the month of October were entering diapause while there was still a plentiful food supply available.

Individuals of a natural population begin leaving winter diapause during the months of March and April, but it is not until June or July that large larval populations can be found.

C. lacinia exhibits what is termed a "long day" response, i.e., one to two weeks are required to leave diapause after the temperature has been raised (Lees, 1955, p. 16). During this period, the larvae have the ability to feed and take in water and frequently do. After leaving diapause, feeding is sporadic, and a longer period of time is required to reach larval maturity than would occur in normal summer larvae at this stage of development.

Adult females attach their eggs underneath mature sunflower leaves in clusters (one to a leaf) one to three egg layers deep. The eggs of each layer are closely packed, except those of the outer layer which may be scattered and lying on their sides. The egg is

approximately 0.5 mm in diameter and 0.6 mm in length, soft bodied, flattened at the top, and obovoid toward the end attached to the leaf. It changes in color from a yellow-green, just after oviposition, to a deeper yellow a few days later, and then to gray before larval emergence.

Some indication of the birth rate and the potential rate of increase can be obtained from the data of six laboratory matings given in Table I. It can be seen that, under laboratory conditions, one female can leave as many as seven egg clusters within a five day period, resulting in up to 1166 surviving offspring (i.e., mating 23b).

Under laboratory conditions, three days are required from adult emergence to the production of the first egg cluster of the next generation. This includes the extra day required by the female, as compared to the male, in the pupal stage (see Table I), one day for sufficient hardening of the adult genitalia before mating is attempted, and one day from copulation to the deposition of the first egg cluster. Thus, a cycle, from the first egg cluster of a mating to the next first egg cluster resulting from the mated individuals within the cluster can be completed under laboratory conditions in approximately 32 days. Assuming the same amount of time from adult emergence to the deposition of the first egg cluster, the same cycle can be completed under field conditions in as few as 25 days.

Adult females in a beginning population, at an area with a high density of sunflower plants, will oviposit near the base of the plant

and, frequently, in such a manner that the first three instars are hidden from easy observation by a sampler walking through the field. When the larval population becomes larger, individuals can be found feeding along the entire length of the plant, except for the young leaves near the top.

The young larvae are leaf skeletonizers and are gregarious, feeding in tightly packed colonies underneath a leaf. Movement of the colony from a skeletonized leaf is usually to adjacent leaves or those growing higher on the plant. During this migration the family unit may split into two or more groups, but a tightly packed feeding group is reestablished once another leaf is reached. Upon reaching the last instar, the larvae begin to disperse individually, breaking up the gregarious feeding units, and eating whole sections of a leaf rather than skeletonizing it.

Tachinid flies and chalcid wasps have been observed to parasitize only last instar larvae. A caterpillar parasitized by a tachinid can be easily recognized by the presence of minute (0.5 mm or less), white, elliptically shaped eggs attached to its dorsal spines. During the research a field observation was made of a small fly inspecting (on the wing) a tightly packed second instar colony of caterpillars on the upper surface of a cocklebur leaf. During the inspection all members of the colony were seen lashing about the anterior halves of their bodies in jerky movements until the fly left. Thus, it may be that an advantage, in the form of protection against predation, may be enjoyed by individuals belonging to a group.

Table I. Life history data from laboratory reared progenies.

Mating Number	Duration of Larval Stage (in days) ♂	♀	Duration of Pupal Stage (in days) ♂	♀	Total Number of Egg Clusters Oviposited on Successive Days * V-29	V-30	V-31	VI-1	VI-2	VI-3	VI-4	VI-5	Average Duration in the Egg Stage (in days)	Average Number of Offspring per Cluster
22b	15	15	5	6	-	1	1	2	1	1	-	-	7.7	180
22c	14	15	6	5	1	-	1	1	-	-	-	2	7.3	152
23a	14	15	6	6	-	1	2	2	2	1	-	1	7.8	95
23b	15	15	5	6	-	1	2	-	2	2	-	-	7.9	167
23c	14	15	6	5	-	1	1	-	2	-	-	-	8.0	264
23e	14	15	6	6	-	1	2	-	1	1	1	1	7.7	206

* Copulation in each mating was performed on May 28, 1967.

DESCRIPTION OF LARVAL, PUPAL, AND ADULT STAGES

The three larval forms with which this research is concerned are shown in Plate I. These resemble the nigra, bicolor, and rufa forms reared by Edwards and described by Cockerell in 1893 (Edwards, 1893).

Nigra is the black form, variable in the number of minute white spots dotted over the body surface. Another variable feature is a small yellow ring around the base of each mid-dorsal spine. In some individuals it is almost absent while in others it is very conspicuous.

Bicolor differs from nigra in having a mid-dorsal orange band extending the length of the body. This banded appearance is derived from large orange areas that are variable in size and pattern and occur one to each body segment, except for the prothoracic and anal segments.

The last form, rufa, is completely orange except for variable amounts of black pigment restricted to the segmented areas of the last instar larva. In the early instar larva this pigment may be diffused between body segments and be present to such an extent that it can easily be mistaken for a bicolor. However, in the last instar the two forms are easily distinguishable.

The chrysalis, or pupa, is variable in the number and extent of black markings and in the presence of a creamy white or light yellow background coloration. A continuous transitional variation exists between the extremes of a pupa nearly devoid of black markings to one

almost blackened by them. The white and yellow color phases are discrete, not sex-linked and may, therefore, be considered polymorphic. However, some type of correlation exists between the background coloration and the amount of black markings since heavily marked pupae are never yellow and, alternatively, those nearly devoid of markings are never white. Two empty pupal cases illustrated in Plate III exhibit the extreme types of variation possible in black markings. The blackened abdominal portions are not part of the pupal coloration but resulted from material excreted by the emerging adults.

Wing coloration and pattern are extremely variable characters throughout the distributional range of C. lacinia. Higgins (1960) recognizes four major forms based on superficial facies: C. l. lacinia (Geyer), C. l. adelina (Staudinger), C. l. crocale (Edwards), and C. l. saundersi (Doubleday). He does not consider these as subspecies although he uses the trinomial nomenclature to conform with lepidopterist custom. Within and outside of these categories are 16 other named varieties, and many of these plus the four major forms have a distribution either restricted to or including Central America.

Higgins feels that the ranges of color forms are elaborated as components of different mimetic or cryptic color associations. For example, the nominate form C. lacinia is found to be a mimic of the Ithomiine models Napeogenes larina Hewitson and Ceratinia callispila Bates, while C. l. nigrescens and C. l. adelina are held to be involved in cryptic color associations.

The form C. l. saundersi occurs over the entire range of the

species and is modified into the form C. l. adjutrix Scudder in Texas and Arizona. Throughout the southwestern States, except possibly eastern Texas, ranges C. l. crocale under which C. l. rufescens Edwards and C. l. nigrescens Wright are considered as variations by Higgins. Progeny from a single mating (mating number 12a in Table II) produced adults resembling C. l. adjutrix, C. l. crocale, C. l. rufescens, and C. l. nigrescens and are shown in Plate II. Dos Passos elevates these to the subspecific level (personal correspondence), but his treatment is questioned. Not only were the forms shown in Plate II obtained from a single mating, but also their existence as discrete types is questioned since other individuals present in the same progeny exhibited a graded range of variation between each form. This poses a classification problem with respect to possible genetic studies of adult types.

Higgins and dos Passos also disagree on the authorships of C. l. rufescens and C. l. nigrescens. Those cited by dos Passos (1964) were used in Plate II.

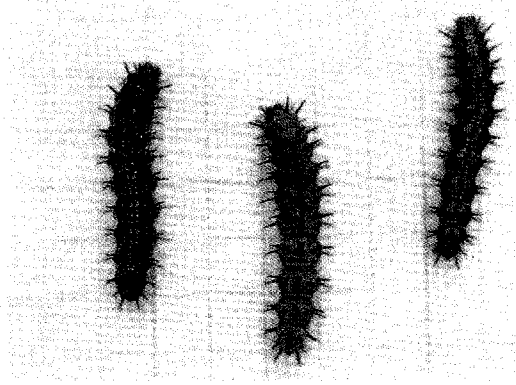

Plate I. Last instar larval color forms. From left to right: nigra, bicolor, rufa. Square scale of paper substrate: 1/8"

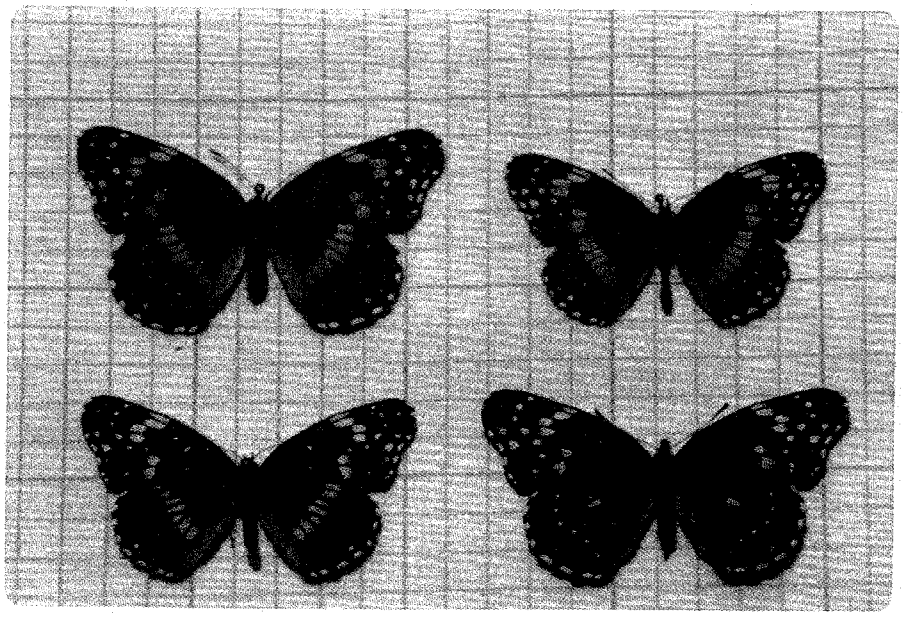

Plate II. Adult color forms. From left to right and top to bottom: adjutrix ♀, rufescens ♂, crocale ♂, nigrescens ♀. Square scale of paper substrate: 1/8"

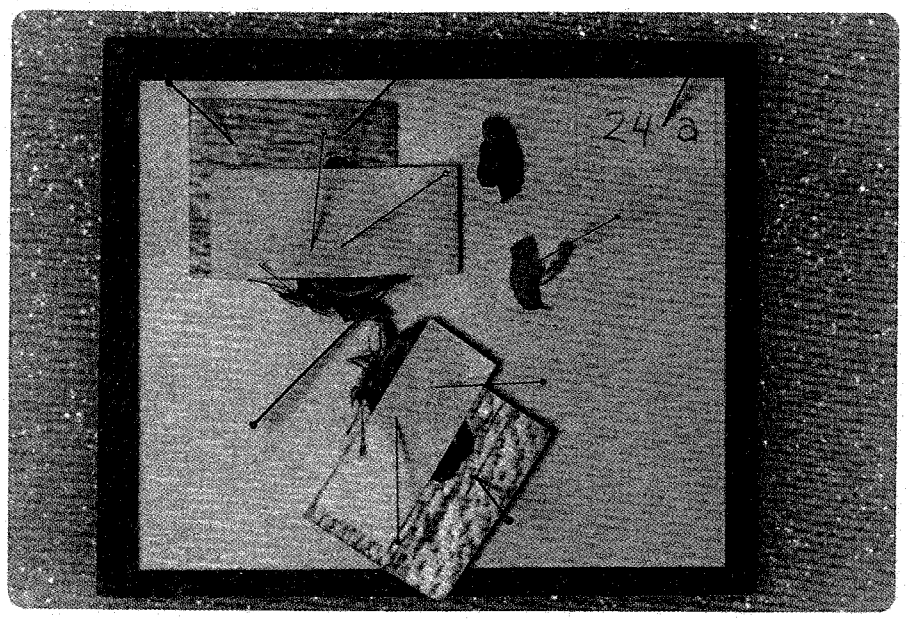

Plate III. Modified hand-pairing technique.
Top: female. Bottom: male.

INHERITANCE OF LARVAL COLOR FORMS

Materials and Methods

Adult pairings were made representing the six possible combinations of larval phenotypes, as shown in Table II. Larvae were reared only on sunflower plants, from the field, which were closely inspected for predators and other C. lacinia eggs and larvae before being used. A mixing of individuals between different sibships was prevented by enclosing the plant, or covering the container of the plant, with a 1/32 in. mesh nylon netting. All sibs of a mating were reared together until the last instar, whereupon a count of larval types was made. Counts at any earlier instar could have led to error since, in some early instar individuals, a bicolor can easily be mistaken for a nigra and a rufa for a bicolor. Individuals were then segregated by larval type and, upon pupation, those that were to be used for mating purposes were separated from one another, so that virgin females would be available.

Separate larval counts were made of egg clusters within a mating. However, these are not enumerated in Table II since the egg cluster data did not differ significantly with respect to the expected ratio of the pooled data.

Mating Techniques

Mating was accomplished in one of two ways: adults were either allowed to mate on their own, or were aided by a modified hand-pairing

technique. In both methods at least 3 days were allowed to lapse from adult emergence before pairing was attempted. Although C. lacinia males may emerge possessing mature sperm, in some Lepidoptera 3 days is the minimum time required for completion of spermatogenesis. During this period the adults were kept in darkness, each occupying a waxed paper cup lined on the inside with paper toweling, bedded with tissue paper, and covered with netting. The food source was sugar water from a 1/2 inch square sponge, inside the cup and attached to the netting.

In the free mating technique the two adults were released into a one gallon metal can (6 inches in diameter and 7 inches high), lined on the inside with light brown paper toweling and covered with netting. It contained a sunflower terminal in a vial of water and a shell vial (3/4 of an inch in diameter and $2\frac{1}{2}$ inches long) filled with sugar water. The shell vial was placed on its side at the bottom and plugged with a sponge that projected half an inch beyond the vial lip. Several layers of absorbent toweling were in contact with the sponge to prevent the formation of a sugar crust.

After being introduced into the can, the adults were taken outside (since they never mated in the laboratory), where they experienced an increased light intensity and a 10 to 15°F rize in temperature (75°F laboratory temperature). If a pair mated at all they usually did so within half an hour after being taken outside.

The parents of progenies 2a, 10b, and 17b were mated in the above manner, but due to its inefficiency in terms of the frequency of successful matings, the hand-pairing technique, illustrated in Plate III,

was used for the remaining crosses. Referring to Plate III, it can be seen that the adults were fastened onto squares of balsa wood, 1/8 of an inch in thickness, by sticking a pin through both the fore wings and the hind wings, previously enclosed in a fold of paper. Since the male, arranged in this manner, refused to mate, it was necessary to squeeze its thorax to the extent that the result was death after copulation. After this treatment the male, in some pairings, immediately clasped the female's genitalia, although it was usually necessary to manipulate the abdomen and extrude its claspers. However, before the thorax was pinched, the female (attached to the balsa square) was fastened to the substrate and its abdomen positioned by guide pins, as shown in the plate, for easy access and to prevent movement during the pairing procedure. Once copulation began, the male was positioned on the substrate and the pair kept undisturbed until mating was completed, this requiring about one hour. Even though a pair may be in copulation, the correct abdominal juxtaposition is required for successful fertilization. The juxtaposition shown in Plate III approximates that of paired adults under natural conditions.

After copulation the female was released into the metal can described above, and during the ovipositional period a constant illumination and a temperature of 80°F were maintained by using an incandescent bulb.

Larval Rearing

An egg cluster deposited underneath the leaf of a sunflower terminal was allowed to remain there until one day before larval emergence, at which time the leaf portion containing the cluster was transferred to a fresh terminal. If the original terminal started to die before the above transfer, the portion containing the cluster was removed, taped to a section of notecard paper and kept in a plastic petri dish. This procedure was necessary, since the eggs would otherwise become trapped in a curled dried leaf. However, this method resulted in lost data in a number of crosses due to egg desiccation. It has since been learned that this problem can be solved by placing, inside the petri dish, a blotter moistened with water containing a little propionic acid to prevent molding (personal discussion with Killian Roever).

The progenies of crosses 2a, 10b, and 12a were reared in the field on sunflower plants enclosed in netting. The netting was constructed in the form of a cylinder (21 inches in diameter and 40 inches high) and in such a manner that the two open ends could be tightened around the plant by pull-strings. At the base of the plant, a 6 inch high sheet of aluminum foil was wrapped around the stem and, centered in the middle and on the outside surface, a 2 inch wide band of cotton swathing was attached. This was necessary to keep out an unidentified ant species, red in color and about 1/16 of an inch long, that readily devoured larvae (at all stages of development) being reared in the netting. However, this ant species did not appear to

affect, in the same manner, natural colonies feeding in the field. When the last instar was reached, the progenies were brought into the laboratory, segregated by larval type, and fed until pupation.

Larvae reared in the laboratory were constantly illuminated and maintained at an 80°F temperature by an incandescent bulb. The larvae, from a single egg cluster, were reared in a waxed paper container (5.125 inches high, 4.875 inches wide at the top, and 3.875 inches wide at the bottom), lined on the inside with brown wrapping paper, and covered at the top with netting. A hole was punched through the center of the bottom so that the stem of a sunflower terminal could be inserted into a jar of water. Any space between the stem and the rim of the hole was plugged with cotton to prevent contamination between progenies by wandering larvae. This type of container was also used as an ovipositing cage for a fertilized female.

When the individuals of a progeny reached the stage of development where rearing became impractical in these containers, because of the fast rate of sunflower consumption, they were transferred to terminals 10 to 15 inches long. Two or three of these terminals would be grouped together and enclosed in a smaller version of the cylindrical netting described above (7 inches in diameter and 12 inches high) with their cut ends immersed in water.

The progenies of crosses 16b and 17b (see Figure 1) were forced to enter diapause since the season was nearing an end and sunflower was on the way out. This was done by reducing the exposure to light

and lowering the temperature to 75°F. In the spring, when sunflower was again available, progenies were brought out of diapause by raising the temperature of the larvae, inside a glass petri dish (6 inches in diameter), to 88°F by an incandescent bulb. The dish was covered with netting, thereby allowing free air circulation, and contained a sunflower leaf on top of nine layers of paper toweling, thoroughly saturated with water. The leaf was kept alive by inserting the petiole into a slit made in several layers of the toweling. Before leaving diapause, the larvae would usually take in some of the water contained in the toweling and also consume a little of the sunflower.

Results and Discussion of Progeny Data

The data from thirty matings, representing six mating classes (or larval phenotypes of the adults) is given in Table II. The first column titled "Mating Number" is the label assigned to specific mating pairs belonging to the mating class as given in the second column. All possible larval genotypes of adults in each mating class expected in accordance with the proposed genetic mechanism is given in column three. The expected larval ratio in the progeny from parents with these genotypes follows next under the heading "Expected Progeny Ratio". The next two columns contain the observed progeny data of the thirty matings. Other parental genotypes that could give the same F_1 larval ratio are placed in parenthesis besides the first genotype. The probability values that resulted from

chi-square tests based on the inheritance proposed below are in the last column.

The genetic mechanism proposed to explain the observed ratios of the nigra, bicolor, and rufa larval forms is a non-linked, two locus system with the nigra and bicolor determining alleles at one locus and those of the rufa at the other. The dominant allele at the rufa locus, symbolized by the letter R, is epistatic with the nigra and bicolor coloration which are expressed only if its recessive homologue, symbolized by the letter r, exists as a homozygote. The dominant allele at the bicolor locus is symbolized by B and produces the bicolor phenotype, either as a homozygote or a heterozygote. Its recessive allele, symbolized by b, in the homozygous condition gives the nigra form.

The proposed phenotype-genotype relationships are thus as follows: nigra, bb,rr; bicolor, Bb,rr BB,rr; and rufa, bb,Rr Bb,Rr BB,Rr bb,RR Bb,RR BB,RR.

The proposed mechanism is supported, first, by the close agreement of the observed with the expected larval ratios, as is evidenced by the probability values given in the last column of Table II, and, second, by the multiple generation lineage data (Figure 1).

Matings were assigned to specific parental genotypic classes on the basis of the following observations: 1) The observed offspring phenotypes dictated only one possible parental genotypic class. 2) The observed number of offspring from a mating was sufficient to consider the lack of a phenotype in the offspring as an indication

of the lack of expected offspring of such a phenotype. 3) Consideration of the multiple generation lineage data with the above observations dictated only one possible parental genotype.

The first two reasons apply to all matings but 23a, 23b, 23c, 23e, 12a, 26l, 26c, and 26q. A combination of the first and third reasons apply to matings 23a, 23b, 23c, and 23e. In Figure 1 the parental genotypes are not given since this can be obtained from Table II.

In the case of matings 12a, 26l, 26c, and 26q, definitive assignment of a specific genotype was not possible on the basis of the above. These matings were therefore tentatively assigned the genotype that best explained the observed offspring ratios. In none of the 30 matings did any offspring data or lineage relationships contradict the proposed model of inheritance.

Table II. Last instar progeny data.

Mating Number	Mating Class	Possible Parental Genotypes	Expected Progeny Ratio			Total Number of Offspring	Total Offspring of each Phenotype			Minimum Probability Value Associated with the Observed and Expected Ratio
			Nigra	Bicolor	Rufa		Nigra	Bicolor	Rufa	
24d	Nigra x Nigra	bb,rr x bb,rr	1	0	0	228	228	-	-	
27b	"	"	1	0	0	316	316	-	-	
-	Nigra x Bicolor	bb,rr x BB,rr	0	1	0	-	-	-	-	
2a	"	bb,rr x Bb,rr	1	1	0	485	254	231	-	0.20
15a	"	"	1	1	0	123	72	51	-	0.05
15b	"	"	1	1	0	332	156	176	-	0.20
15c	"	"	1	1	0	112	50	62	-	0.20
25l	Bicolor x Bicolor	BB,rr x BB(Bb),rr	0	1	0	161	-	161	-	
10b	"	Bb,rr x Bb,rr	1	3	0	102	22	80	-	0.05
16a	"	"	1	3	0	143	36	107	-	0.95
16b	"	"	1	3	0	87	13	74	-	0.030
22b	"	"	1	3	0	180	40	140	-	0.20
22c	"	"	1	3	0	455	118	337	-	0.50
25i	"	"	1	3	0	82	20	62	-	0.80
25j	"	"	1	3	0	202	62	140	-	0.05
-	Bicolor x Rufa	BB(Bb),rr x BB(Bb,bb),RR	0	0	1	-	-	-	-	
-	"	Bb,rr x bb,Rr	1	1	2	-	-	-	-	
12a	"	Bb,rr x Bb,Rr	1	3	4	857	131	304	422	0.040
21a	"	BB,rr x BB(Bb,bb),Rr Bb,rr x BB,Rr	0	1	1	53	-	26	27	0.80

Table II. (Continued)

Mating Number	Mating Class	Possible Parental Genotypes	Expected Progeny Ratio			Total Number of Offspring	Total Offspring of each Phenotype			Minimum Probability Value Associated with the Observed and Expected Ratio
			Nigra	Bicolor	Rufa		Nigra	Bicolor	Rufa	
-	Rufa x Rufa	bb,Rr x bb,Rr	1	0	3	-	-	-	-	
17b	"	BB(Bb),Rr x BB,Rr	0	1	3	465	-	125	340	0.20
26l	"	bb,Rr x Bb,Rr	1	1	6	121	18	10	93	0.20
26b	"	BB(Bb,bb),RR x BB(Bb,bb),RR								
		" x BB(Bb,bb),Rr	0	0	1	125	-	-	125	
26m	"	"	0	0	1	160	-	-	160	
26o	"	"	0	0	1	258	-	-	258	
26p	"	"	0	0	1	58	-	-	58	
26v	"	"	0	0	1	123	-	-	123	
23a	"	Bb,Rr x Bb,Rr	1	3	12	851	54	155	642	0.80
23b	"	"	1	3	12	1166	79	215	872	0.50
23c	"	"	1	3	12	264	22	45	197	0.20
23e	"	"	1	3	12	206	13	37	156	0.99
26c	"	"	1	3	12	175	13	23	139	0.05
26q	"	"	1	3	12	84	5	13	66	0.50
-	Nigra x Rufa	bb,rr x BB(Bb,bb),RR	0	0	1	-	-	-	-	
-	"	bb,rr x bb,Rr	1	0	1	-	-	-	-	
-	"	bb,rr x BB,Rr	0	1	1	-	-	-	-	
28b	"	bb,rr x Bb,Rr	1	1	2	292	68	73	151	0.50

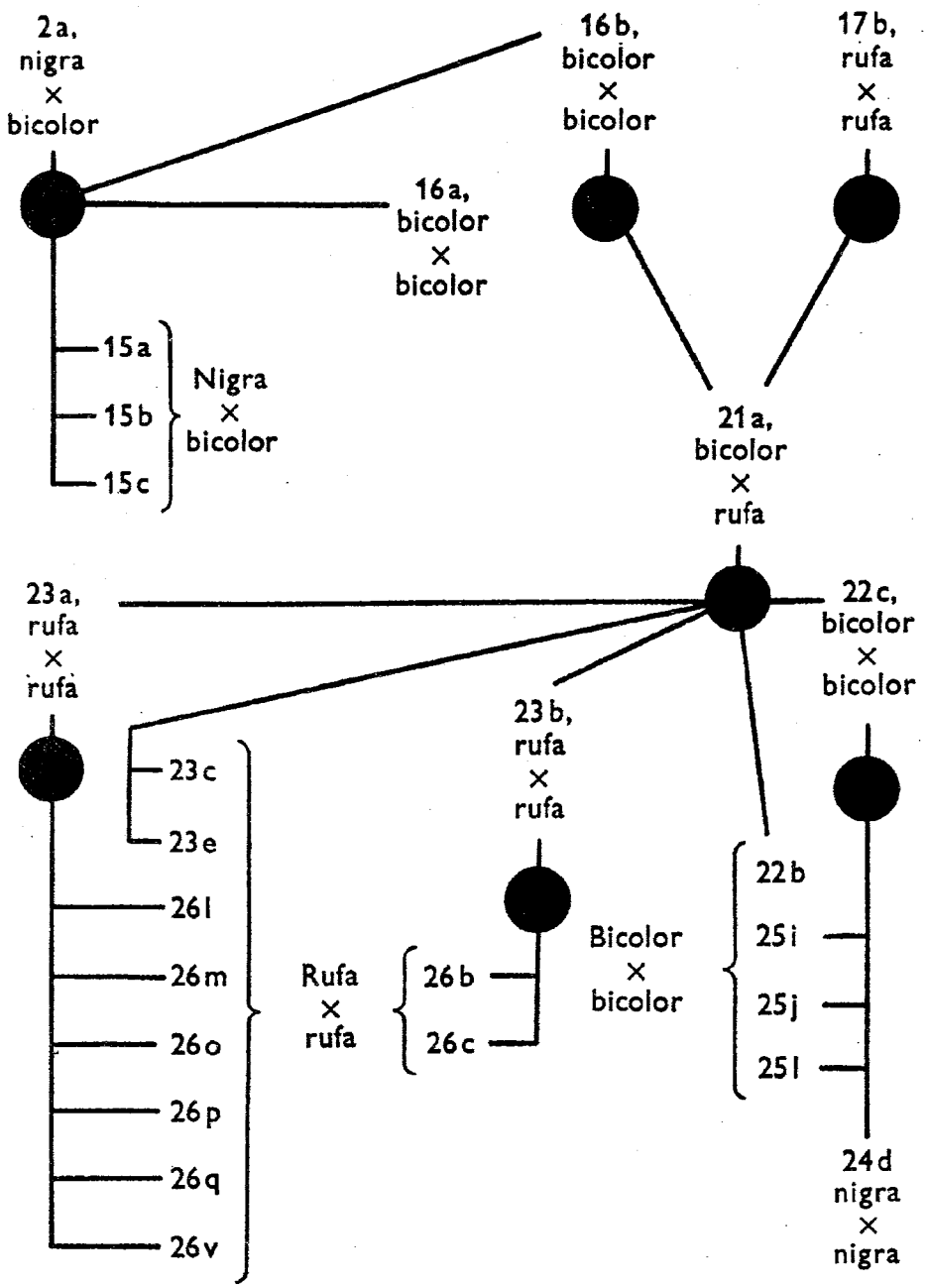

Figure 1. Multiple generation lineage chart.

NATURAL POPULATIONS

Natural larval populations of the Mesa-Chandler-Higley area (see Figure 2) were sampled to obtain larval type frequency estimates and to determine the presence of spacial and temporal heterogeneity.

Sampling Procedure

The objective of obtaining a random sample of larval types was hindered by the large number of offspring that can result from one egg cluster (deposited by a single female) coupled with the gregarious habits of the larvae. In an attempt to diminish this progeny effect, large sample sizes were obtained.

Seven areas were sampled, all in Maricopa County, Arizona, between 1200 and 1400 feet in elevation. Sunflower was the foodplant in all localities. The assigned names and numbers of these areas are given underneath the map of Figure 2, each followed by its location (intersecting street names and the distance from a city or town) and the collection date(s). All samples, except the September 1966 sample, were collected in 1969.

Caterpillars were collected in paper bags and brought into the laboratory for counting. Although second instar larvae acquire distinguishable phenotypes to a degree, a bicolor can easily be mistaken for a nigra and a rufa for a bicolor. Therefore, only 3rd, 4th, and 5th instar larvae were collected. Those caterpillars from the Alma and West Alma localities were released at the site of

collection the next day, in an attempt to minimize population disturbance. The sampling procedure differed in October by the necessity of having to include diapausing larvae so that a large sample could be obtained.

The population data are presented in Tables III and IV. Table III gives the total number of the three larval phenotypes, and their frequencies (relative to the total individuals of a sample), at each locality. Table IV is a refinement of III in that the sample at each collection date is broken down into the following categories: the 3rd, 4th, or 5th instar; questionable instars; or, diapausing larvae.

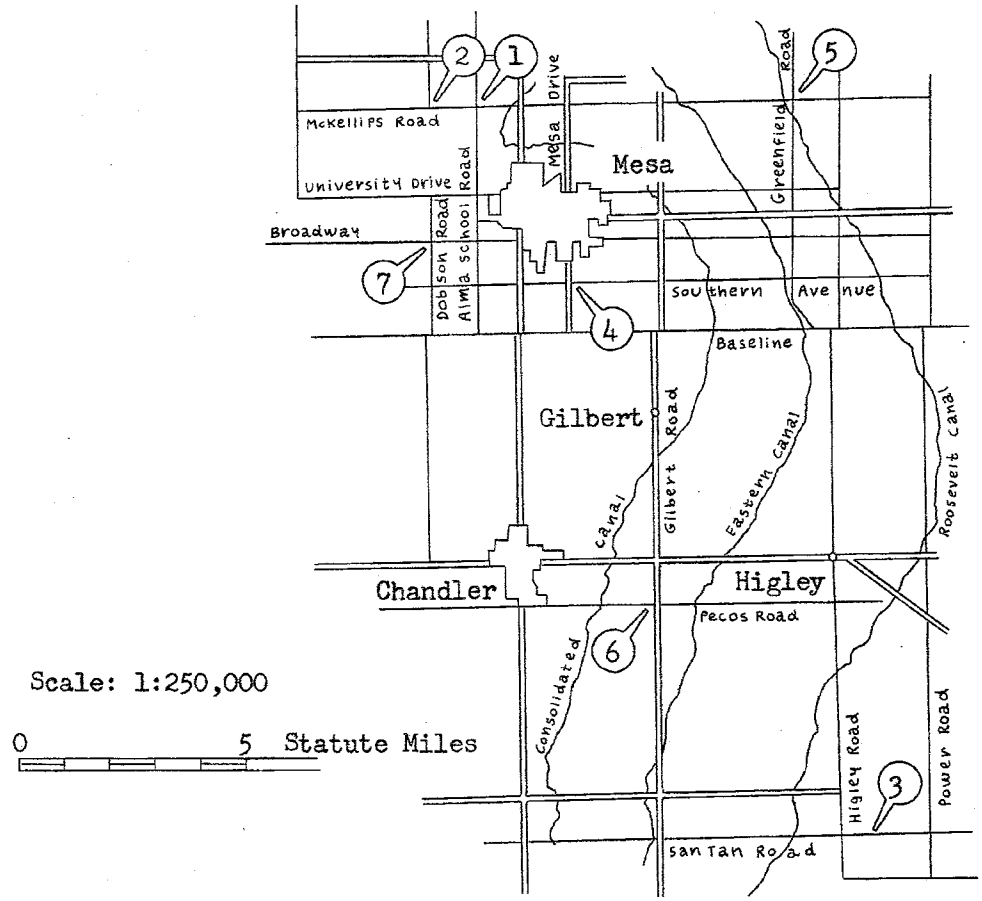

Figure 2. Collection localities of the Mesa-Chandler-Higley area.

1. Alma: Alma School Rd. & McKellips Rd., 2 mi. NW Mesa; September 5-8, 1966, July 13 & 14, 1969, and August 7, 1969

2. West Alma: 1 mi. W of the above locality, July 15-18, 1969 & August 6, 1969

3. Higley: San Tan Rd. & Higley Rd., 10 mi. SE Chandler; October 19, 1969

4. Mesa: Mesa Drive & Southern Ave., Mesa; October 16, 1969

5. Greenfield: Greenfield Rd. & McKellips Rd., 7.5 mi. NE Mesa; October 11, 1969

6. Gilbert: Gilbert Rd. & Pecos Rd., 4 mi. S Gilbert; October 19, 1969

7. Dobson: Dobson Rd. & Broadway, Mesa; October 19, 1969

Table III. Total number and frequency of each larval type within sample dates.

Locality	Sample Date	Total Individuals of Each Phenotype within Sample Dates & Their Associated Frequencies						Total Number in Each Sample Date
		Nigra		Bicolor		Rufa		
		Larval Number	Freq.	Larval Number	Freq.	Larval Number	Freq.	
1. Alma	September, 1966	997	.248	2513	.625	513	.128	4023
	July, 1969	386	.117	2462	.744	460	.139	3308
	August, 1969	238	.180	742	.561	342	.259	1322
2. West Alma	July, 1969	590	.186	2036	.641	552	.174	3178
	August, 1969	271	.229	685	.579	227	.192	1183
3. Higley	October, 1969	314	.237	797	.601	215	.162	1326
4. Mesa	October, 1969	63	.037	1296	.751	366	.212	1725
5. Greenfield	October, 1969	81	.116	388	.556	229	.328	698
6. Gilbert	October, 1969	-	-	62	.861	10	.139	72
7. Dobson	October, 1969	43	.291	68	.460	37	.250	148
Combined Collections (September 1966 date excluded)		1986	.153	8536	.659	2438	.188	12960

Table IV. Total number and frequency of each larval type within instars.

Locality	Sample Date	Instar	Total Individuals of Each Phenotype & Their Associated Frequency within Instars: Nigra Larval Number	Nigra Freq.	Bicolor Larval Number	Bicolor Freq.	Rufa Larval Number	Rufa Freq.	Total Number of Each Instar
1. Alma	September, 1966	3rd	502	.287	1017	.582	228	.131	1747
		4th	189	.220	512	.596	158	.184	859
		5th	156	.405	169	.439	60	.156	385
		?	150	-	815	-	67	-	1032
	July, 1969	3rd	135	.112	1025	.851	45	.037	1205
		4th	228	.225	633	.626	151	.149	1012
		5th	23	.029	516	.647	258	.324	797
	August, 1969	5th	238	.180	742	.561	342	.259	1322
2. West Alma	July, 1969	3rd	198	.283	363	.519	138	.198	699
		4th	97	.142	412	.603	174	.255	683
		5th	295	.164	1261	.702	240	.134	1796
	August, 1969	5th	271	.229	685	.579	227	.192	1183
3. Higley	October, 1969	3rd	9	.091	35	.353	55	.556	99
		4th	51	.144	291	.820	13	.036	355
		Diapause	254	.291	471	.540	147	.169	872
4. Mesa	October, 1969	3rd	-	-	251	.734	91	.266	342
		4th	63	.046	1045	.756	275	.199	1383
5. Greenfield	October, 1969	3rd	-	-	93	.727	35	.273	128
		4th	81	.142	295	.518	194	.340	570
6. Gilbert	October, 1969	4th	-	-	13	.722	5	.278	18
		Diapause	-	-	49	.907	5	.093	54
7. Dobson	October, 1969	4th	6	.118	8	.157	37	.726	51
		Diapause	37	.381	60	.619	-	-	97

Results and Discussion of Population Data

Throughout the following discussion, unless otherwise stated, the phenotype frequencies referred to are based on calculations restricted to a single locus. The rufa and non-rufa (i.e., the bicolor and nigra larval types) frequencies are based on the total number of individuals exhibiting each phenotype. The bicolor and nigra frequencies are calculated from only the non-rufa individuals observed and, therefore, are based on a smaller sample size. Utilizing the data from Table III, the non-rufa and nigra phenotype frequencies, calculated in this manner, are given in Table V. The corresponding frequencies of the rufa and bicolor larval types are not given, but, if desired, these can be respectively obtained by subtraction from unity.

The data of Table III (excluding the September 1966 sample), was also used in 2x2 contingency table tests. The hypothesis tested was that each of the two larval types, at a single locus, were members of the same population, either with respect to two different sample dates or two localities. Each contingency table test was also considered a test of the frequency homogeneity of each phenotype with respect to the above two categories. As a result, acceptance of the hypothesis, using a 0.025 significance level, was interpreted to mean that the two differing frequency values of a single phenotype were chance deviations from a common value.

These tests, 10 in total, and the resulting chi-square and probability values, are given in Table VI. The two sample dates or

localities against which the phenotypes were tested are given under the column heading "Row Elements". For the first 8 tests, the sample dates were July and August, and the localities were Alma and West Alma. For the last two tests, the combined months of July and August were considered one sample date and October the other. It should be noted that the Alma and West Alma locality combination can be substituted for the July-August sample date and the remaining localities (Higley, Mesa, Greenfield, Gilbert, and Dobson) for the October sample. Identical chi-square and probability values result since the first two localities were sampled only during July and August, while the remaining were sampled in October (see Table III). The locality or sample date from which the data were drawn for use in a contingency table test is under the first column heading of Table VI.

Looking at the results of the first 8 tests, it can be seen that the hypothesis was accepted in only two; the first, or the rufa and non-rufa pair vs. the two sample dates at the West Alma locality; and the eighth, or the bicolor-nigra pair against the two localities during the month of August.

Three factors are believed to have played a part in the heterogeneity indicated by the remaining 6 tests. Keeping in mind that these apply to significant phenotypic, not allelic, frequency heterogeneities, they are: a) the fecundity effect, or the large number of offspring that one female can contribute to a population (see Table I), b) the progeny effect, or the large number of offspring in a colony coupled with their gregarious habit, and c) the neighborhood

effect, or limited intergeneration dispersal of adults.

The fecundity effect is different from the progeny effect in that it is not an inherent error of the sampling procedure but is a natural phenomenon in small populations of these larvae. The fecundity effect would be expected to increase frequency heterogeneity between broods since the progeny contribution of one female, in a small population, would be a significant factor altering phenotype frequencies. It is believed that this effect may have influenced the outcome of the frequency tests between broods (numbers 2, 3, and 4) at each locality for two reasons. First, a check of the Alma locality a month previous to the July sample may have been taken from a small population derived from a limited number of parents. Second, 7 days at most separate the 5th from the 3rd instar and yet, referring to Table IV, significant heterogeneity can be seen in the frequency of a phenotype (here the frequency of each larval type is based on the total sample size within a particular instar) between instars within sample dates.

The progeny effect is related to the problem of obtaining a random sample of offspring from various matings and would affect statistical tests of small populations to a lesser degree than would the fecundity effect, since nearly all individuals in the population could be collected and counted. The reverse would occur in a large population since the contribution of one female would affect frequencies to a lesser degree.

Assuming that the samples represent actual phenotypic frequen-

cies at each locality, then the heterogeneity between localities may be due to a limited intergeneration dispersal of adults. However, this is related to the fecundity effect and the founder phenomenon, discussed below, and, therefore, cannot be isolated as a single factor.

Yearly frequency changes may possibly be affected by other factors. From observations in the field, the feeding season ends with a large number of larvae entering diapause. However, the spring population is small, and it is not until June or July that a buildup is noticeable, indicating a high death rate in either diapausing or post-diapausing larvae. Because of this spring drop in population size, a phenomenon similar to the founder principle (Mayr, 1963, p. 211) may occur, i.e., phenotypic frequencies may change due to gene frequency changes resulting from the population's sampling error. This phenomenon and the fecundity effect are related in the sense that both occur in small, as opposed to large, populations.

With respect to the tests between localities (numbers 5, 6, 7, and 8), it is not known whether the Alma and West Alma localities represent two panmictic populations or one. The latter is suspected, although the frequency homogeneity indicated in the eighth test does not necessarily prove this. However, widely separated localities (like the Higley, Mesa, Greenfield, Gilbert, and Dobson areas) would represent separate gene pools, and frequencies between localities would be expected to differ, if adult dispersal is minimal.

Based on the September 1966 sample, the 1969 Alma and West Alma

samples, and the last two contingency tests, it appears that each population, in general, tends to maintain each of the four phenotypes at a characteristic frequency (i.e., a parameter). From Table V it can be seen that the non-rufa and nigra phenotype frequencies from the September 1966 sample generally agree with the values for the July and August 1969 samples at both localities. The contingency table tests are in support, if considered after the Alma and West Alma localities are substituted for the July-August sample date, and the remaining five localities for the October sample date (as was previously stated could be done). Test number 9 resulted in a probability range of 0.025-0.010 and a 5.35 chi-square value, but the probability was less than 0.010 in all other tests, in which the hypothesis was rejected, and the minimum chi-square value obtained was 13.27 (test number 2). Under these circumstances, it is felt that, although the test hypothesis was rejected in number 9, in conjunction with test number 10 (in which the hypothesis was accepted), it supports the above statement.

Because of the previously stated factors that can possibly influence a population sample, the results of the last two tests (Table VI) suggest that the pooled data, from all localities, are a better estimate of the 1969 phenotype frequency parameters of the Mesa-Chandler-Higley area than any single locality. After pooling the data, the following frequency estimates are obtained (Table V): rufa, 0.188; non-rufa, 0.812; bicolor, 0.811; nigra, 0.189.

In considering a possible maintenance factor (or factors) of the

larval polymorphism, the following question can be asked: is selection operating continuously or does it affect a population only part of the year, for example, in the spring when the larvae are coming out of diapause? On this nothing can be inferred from the data, but, with the assumption that selection has already operated and the population at each locality is in equilibrium (requiring only one panmictic generation when a single locus is considered), gene frequencies have been calculated for the data in Table III. The results are given in Table V. The frequency of the recessive allele at the rufa and bicolor locus was obtained by taking the square root of the non-rufa and nigra frequencies respectively (these are the homozygous recessives). From this the frequency of the alternate allele was obtained by subtraction from unity. Because of the epistasis at the rufa locus, the gene frequency calculations at the bicolor locus were based on a reduced sample size.

Using the phenotype and gene frequency estimates from the combined collections (the pooled data), the following facts can be noted:

1. At the rufa locus the estimated frequency of the heterozygote, which is expressed as the rufa phenotype because of dominance, is 0.178. Because of the low frequency of the rufa larval type (i.e., 0.188), approximately 95% of all rufa individuals are heterozygotes.
2. At the bicolor locus the estimated frequency of the heterozygote is 0.491, which is an approach to the maximum value possible in a population at equilibrium (i.e., 0.500).

Approximately 61% of all bicolor individuals are heterozygotes.

3. The most interesting frequency observation, relative to a single locus, is the occurrence of the rufa and nigra larval types at approximately the same frequency, the values being 0.188 and 0.189 respectively.

Due to the lack of more research results, a maintenance mechanism of the polymorphism cannot be proposed. However, the 1966 and 1969 phenotype frequency values suggest temporal stability, and the near identical frequencies of the rufa and nigra larval types (mentioned above) possibly suggest an interaction of genotypes.

Table V. Phenotypic frequencies of separate loci and estimated allelic frequencies.

Locality	Sample Date	Total Individuals	Total Individuals of Non-Rufa Phenotype	Frequency of Non-Rufa Phenotype	*Rufa-Locus Gene Frequencies		Total Individuals of Nigra Phenotype	Frequency of Nigra Phenotype	**Bicolor Locus Gene Frequencies	
					p	q			r	s
1. Alma	September	4023	3510	.872	.066	.934	997	.284	.467	.533
	July	2848	2848	.861	.072	.928	386	.136	.632	.368
	August	1322	980	.741	.139	.861	238	.243	.507	.493
2. West Alma	July	3178	2626	.826	.091	.909	590	.225	.526	.474
	August	1183	956	.808	.101	.899	271	.283	.468	.532
3. Higley	October	1326	1111	.838	.085	.915	314	.283	.468	.532
4. Mesa	October	1725	1359	.788	.112	.888	63	.046	.979	.022
5. Greenfield	October	698	469	.672	.180	.820	81	.173	.584	.416
6. Gilbert	October	72	62	.861	.072	.928	-	.000	1.000	.000
7. Dobson	October	148	111	.750	.134	.866	43	.387	.378	.622
Combined Collections (September date excluded)		12960	10522	.812	.099	.901	1986	.189	.566	.434

* p frequency of R allele, q frequency of r allele
** r frequency of B allele, s frequency of b allele

Table VI. Chi-square and probability values of 2x2 contingency table tests, each with the respective row and column elements at a specific locality or sample date.*

Locality or Month Characterization of Each Contingency Table Test	Row Elements	Column Elements	Chi-Square Value	Probability Value
1. West Alma	July : August	Rufa : Non-Rufa	1.94	.20 - .10
2. West Alma	July : August	Bicolor : Nigra	13.27	.01 - .00
3. Alma	July : August	Rufa : Non-Rufa	94.41	.01 - .00
4. Alma	July : August	Bicolor : Nigra	61.55	.01 - .00
5. July	West Alma : Alma	Rufa : Non-Rufa	14.77	.01 - .00
6. July	West Alma : Alma	Bicolor : Nigra	74.10	.01 - .00
7. August	West Alma : Alma	Rufa : Non-Rufa	15.87	.01 - .00
8. August	West Alma : Alma	Bicolor : Nigra	4.12	.05 - .025
9. Combined Localities	July & August : October	Rufa : Non-Rufa	5.35	.025- .01
10. Combined Localities	July & August : October	Bicolor : Nigra	3.79	.10 - .05

* Each probability value is based on 1 degree of freedom

SUMMARY

1. Three larval color forms of the butterfly Chlosyne lacinia (Geyer) occur in natural populations. The genetics of these forms and also their phenotypic frequencies in natural Arizona populations of the Mesa-Chandler-Higley area were studied.
2. The genetic mechanism proposed is a non-linked, two locus, epistatic system. The bicolor and rufa determining alleles are dominant over their recessive homologues with the dominant rufa allele epistatic over the bicolor locus.
3. From the phenotypic frequency study of natural populations, a high degree of spacial and temporal heterogeneity was indicated. Three factors were postulated to have contributed to the observed heterogeneity:
   a) the fecundity effect, or the large number of offspring that one female can contribute to a population,
   b) the progeny effect, or the large number of offspring in a colony coupled with their gregarious habit, and
   c) the neighborhood effect, or limited intergeneration dispersal of adults.

   The fecundity effect is not an inherent error of the sampling procedure but is a phenomenon of small populations. The progeny effect is related to the problem of obtaining a random sample of offspring from various matings.
4. It was proposed that yearly phenotype frequency changes were

caused by a phenomenon similar to the founder principle. Because of the spring drop in population size, frequencies may change due to gene frequency changes resulting from the population's sampling error.

5. It appears that populations generally tend to maintain each phenotype at a characteristic frequency. The pooled data from the Mesa-Chandler-Higley area produced the following phenotype frequency estimates (relative to each locus) for the year 1969:

   Rufa locus: rufa, 0.188; non-rufa, 0.812

   Bicolor locus: bicolor, 0.811; nigra, 0.189.

6. The phenotype frequency data from two years (1966 and 1969), at a single locality, suggest temporal stability.

7. An interesting frequency observation from the pooled data was made. Relative to a single locus, the rufa and nigra larval types occur at approximately the same frequency, the values being 0.188 and 0.189 respectively, thus suggesting an interaction of genotypes.

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BIOGRAPHICAL SKETCH

Stanley Adrian Gorodenski was born in Niagara Falls, New York, on January 8, 1943. He received his elementary education in the Erie, Pennsylvania, Public Schools and his secondary education in the Roswell, New Mexico, and Mesa, Arizona, Public Schools. In 1961 he entered Arizona State University, graduating in 1968 with a Bachelor of Science degree in Zoology. Since September, 1968, he has been working toward the Master of Science degree in Zoology at the same school.