

INHERITANCE IN LADY BEETLES

II. The spotless pattern and its modifiers in *Hippodamia convergens* and their frequency in several populations*

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IF knowledge of the genetics of color pattern in the Coccinellidae is to be used for analysis of natural populations, particularly geographic races, of this family, and through them for the study of evolution, it is desirable that the facts relating to a widely distributed species be obtained early. For the Americas, one species which eminently fulfills this requirement is *Hippodamia convergens* Guer.

The Usual Elytral Pattern

The most common pattern of this species consists of six black spots on each elytron, zigzagging from an anterior outer (humeral) spot back to a spot (the apical one) near the posterior tip (Figure 5A). There is often a slight stripe shared by the two elytra at their inner front corners (the scutellar stripe), but this is ignored because the shadow in the crevice between the elytra makes it difficult to judge the size of the black area when this is small.

The most striking deviation from this "wild-type" pattern is one which may be called "spotless." The latter variety may be actually spotless (Figure 5B), but more often some of the spots may be present, though greatly reduced (C). The anterior three spots are more often present in the spotless variety than are the rest, but no one of the six spots is *always* absent. Indeed, all six spots may be present in the same spotless beetle, though most or all of them are much reduced. How to recognize the spotless individuals under these circumstances is discussed later in this paper.

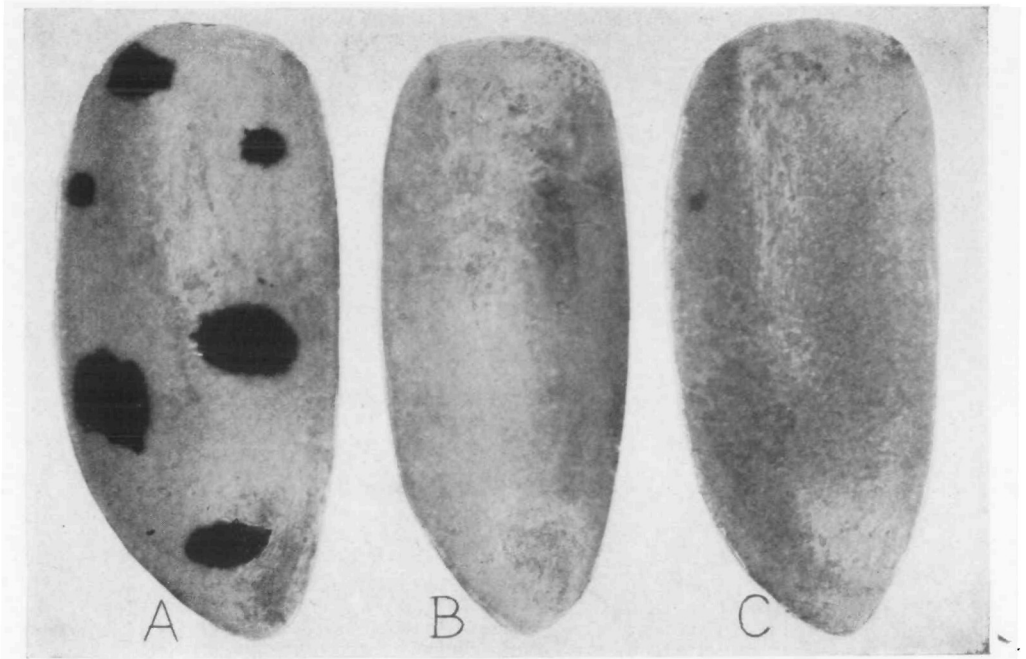
Experiments to test the inheritance of the spotless and spotted pattern were performed with beetles collected in Ann Arbor, Michigan, some obtained from

Placerville, California (Mr. E. M. Fields), and, doubtfully, some which were extracted from earlier crosses involving beetles from Placerville, Yosemite Valley (obtained through the courtesy of Supt. Frank A. Kittredge, of Yosemite National Park), and certain other forms. The crosses dealing with these three groups are reported separately in Table I.

The first cross was made with a spotless female and a spotted male collected in Ann Arbor. The female was not assuredly virgin, but if she had mated previously the chance is very great that the male involved was spotted. The parents in this first cross were lost, but are described in the records as "spotless" and "typically 12-spotted." The experiment is listed as No. 20 in the first line of Table I, where it is shown that the offspring were 21 spotless and 12 spotted. Clearly one of the parents was homozygous, and the next five experiments in the table indicate that it was the spotless one. Spotless \times spotless (Exps. 37, 38, 39) together yielded 74 spotless and 27 spotted, while spotted \times spotted (Exps. 36, 42) yielded only spotted. A further mating of spotted \times spotted (Exp. 53), using progeny of Experiment 36, yielded also only spotted. Spotless is plainly dominant, though the question how complete the dominance is must be raised later.

From the Placerville collection two matings were made to obtain virgin females. One was a pair of spotless beetles (Exp. 264), the other a group of four or five spotted ones (Exp. 265). The two spotless parents were clearly both heterozygous, as was to be expected from the infrequency of that type. Between these two progenies eight single-

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SPOTTED AND SPOTLESS PATTERNS

Figure 5

Left elytra of the lady beetle (*Hippodamia convergens*) showing the normal spotted pattern (A) and the spotless pattern (B and C). In the "spotless" beetle the spots are actually absent more rarely than in the type wherein some of the spots appear (C) but are greatly reduced in size. See Pages 331 and 333-334 for a discussion of the limits of variation in this type.

pair crosses were made,—three of one of the reciprocal crosses, five of the other, as shown in the Placerville section of the table. In seven of these eight crosses the spotless beetle chosen must have been homozygous, while in only one (Exp. 273) was the spotless parent heterozygous. Since the heterozygous spotless progeny of Experiment 264 should have been twice as numerous as the homozygous spotless, the preponderance of homozygous ones among those used in crosses suggests that the choice of individuals for parents was not random. If dominance were not quite complete, and if the least spotted individuals were selected as insurance that they were really of the spotless kind, the choice may have fallen more often on the *SS* genotype than on the *Ss*.

The so-called "extracted" beetles referred to in the last section of Table I were the descendants of earlier crosses,

as described above. The precise nature of these crosses need not detain us here. The beetles used were sufficiently near to the spotless and spotted varieties found in nature to suggest that the same pair of genes was involved, even if accompanied by minor genes at other loci. Experiment 307, from which the extracted beetles were obtained, was obviously the mating *Ss* × *ss*, so that the spotless offspring used in the next four experiments in the table must be heterozygous. Their progeny show them to be such. The spotted beetles from 307 are in like manner shown, in the last four lines of the table, to be homozygous.

Dominance of Spotless

The spotless variety plainly differs from the spotted variety by one gene. How nearly dominant the spotless gene is is not clear from the table, since no details of the spotless pattern are there

given. One observation mentioned above suggests that dominance is not quite complete. Some slight additional evidence on this point is obtainable from the experiments of Table I, for seven spotless parents (Exps. 266 to 272) are there shown to be homozygous, while their 102 offspring must be heterozygous; and six parents (Exps. 273 to 325, as arranged in the table) are demonstrated to be heterozygous, and their 71 spotless offspring must also be heterozygous.

To use this comparison, it is necessary to have some method of rating the extent of the spotting. A rough method, devised early in the experiments and consequently based only on Michigan beetles, was to consider the largest spot yet observed up to that time in each of the six positions as having a value of 4. Smaller spots in each position were rated 3, 2 or 1. The size of spots was ordinarily estimated, but at frequent intervals they were measured, to keep the standards fresh in mind. The darkest beetle possible under this scheme had a rating of $6 \times 4 = 24$. It was later necessary to increase the maximum rating of the spots to 5 or even 6 to accommodate the California beetles, so that presumably a maximum in that region might be $6 \times 6 = 36$. However, relatively few of the beetles in either region attain the maximum in all six spots.

Since the Michigan standard is the better established of the two, and since only relative, not absolute, values are wanted, the experimental beetles referred to above are rated as a percentage of the Michigan maximum, even though all the beetles compared are western derivatives. The seven homozygous spotless parents had a mean rating which is 7.14 per cent of the maximum, while their 102 heterozygous offspring had a mean rating of 9.93 per cent of the maximum. The six heterozygous parents had a mean rating of 12.50 per cent of the maximum, and their 71 heterozygous offspring a mean rating of 13.79 per cent of the maximum. It would be possible to interpret these figures to mean a slight incompleteness of domi-

nance of the spotless pattern, but the difference would be negligible in field studies.

Recognition of Spotless

Since all of the spots may be present in a spotless beetle, the question arises whether there is any overlapping between spotless and spotted. To answer this question the same scheme of measurement described above may be used. However, since it is the anterior three spots which are most often present and relatively the largest in spotless beetles, a sharper contrast between spotless and spotted may be made by considering only the three posterior spots. These are usually the largest ones in a spotted beetle, and relatively the smallest (if present at all) in a spotless one. The maximum aggregate size of these three spots, on the Michigan basis, would be $3 \times 4 = 12$.

All the beetles of Table I have been rated on this scheme. Of the Michigan beetles, no spotless individual had an aggregate rating of more than 2 for the three posterior spots, and no spotted beetle a rating of less than 6 for these spots. Of the California beetles, including those extracted from crosses, no spotless beetle rated higher than 3, no spotted beetle lower than 10, for the three posterior spots. When the classification of a wild population involves only the contrast between these two genes, there appears therefore to be no room for uncertainty.

Modifying Genes

In certain lines of descent, however, the distinction between spotless and spotted is not so clear. One such line has been investigated through seven generations. In the light of data to be presented, the fluctuations observed in the pattern are interpreted as the result of a number of modifying genes.

The line referred to started with a female which when captured was regarded as spotless but which proved to possess the first four spots (counting from the front), and a male which was regarded as typically spotted though probably not having the maximum size of

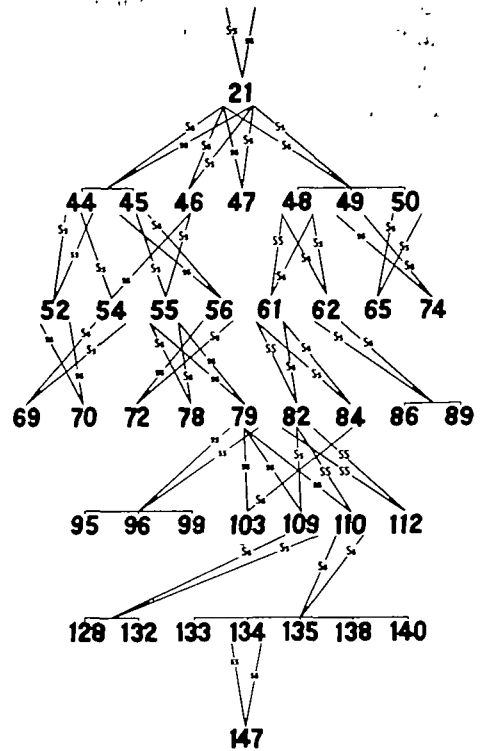
all six spots. Both of these adults were lost, so that descriptions now are based on records and memory. The female may have mated before, but almost certainly with a spotted male if she had.

The course of the experiments dealing with the descendants is outlined in Figure 6. In explanation of that diagram, it is important to point out that the crosses made are not always the most desirable ones, but are the ones which succeed. In the long run, many attempted crosses fail. Though most early matings, starting with beetles taken in nature, are fertile and produce numerous offspring which mature, there is a progressive deterioration in later generations. Fewer and fewer matings are successful, more and more eggs fail to hatch, and mortality becomes higher and higher in all stages from early larvae to pupae. This decline in "vigor" has been noted in every series of experiments which I have so far conducted with coccinellids. The gaps in the series of experiment numbers in Figure 6 represent in general the experiments which failed. The reason may be inbreeding in the presence of semilethals, or the cumulative effect of unsuitable conditions in the laboratory.

Because of this deterioration, one is discouraged from waiting to establish homozygous strains before making crosses. Likewise, the separation, by selection, of various types out of an original complex genotype is largely prevented.

Detailed Data

For an understanding of the modifying genes involved in the experiments in Figure 6, it seems necessary to record the pattern of every parent and all of their offspring. This is done in Table II for the whole series of experiments. Each beetle is represented by six digits measuring its six spots on one elytron, beginning with the anterior outer (humeral) spot and zigzagging back, as indicated earlier, to the most posterior (apical) spot. The measure is on the basis of 4 for the maximum size yet observed when the scheme was devised, 0 for no spot, as explained in an earlier



A GENEALOGY OF THE EXPERIMENTS

Figure 6

This chart shows the course of the experiments presented in Table II. The genotypes of some of the parents are only tentative. The gaps in the experiment numbers, in general, show the experiments which failed.

section. A strictly spotless beetle is thus rated 000000, a spotted one with maximum spots 444444.

Each enclosed space in Table II represents one experiment. At the top are the ratings of the two parents, the female being given first. Below, in two columns, are their offspring. The source of the parents may be ascertained from Figure 6. A question mark following the rating of a parent indicates that this beetle is no longer available, and that its rating is taken from recorded descriptions which in the early experiments were less accurate. In two early experiments a lost parent was recorded simply as typically spotted, and no rating is now possible. A number following and sepa-

rated by a hyphen from the rating of any of the offspring means the number of offspring having that particular pattern. In experiment 45, intended at first as a stock, the surviving parents are all males; the females were variously spotted. All other experiments started with a single pair, of which the female (except perhaps in Exp. 21) was virgin. The offspring are arranged roughly in order of aggregate size of spots, based primarily on the last three spots, secondarily on the first three.

Interpretation of Ratings

It is clear from such experiments as 110 and 133 (Table II) that the gene for spotless was borne by one of the parents in the first experiment (21), and that parent must have been the mother. From Experiments 70, 79, 95, 96, 99 and 147 it is apparent that the typical spotted pattern was also involved in that first cross. It is presumably a fair assumption that the array of patterns produced in most of the other experiments is the result of other genes modifying the expression of the spotless, or the spotted, or both. Which one is modified, and to what extent?

In the six all-spotted progenies named just above, the lowest aggregate rating for the three posterior spots, which as explained before are the most distinctive ones, is 10 (out of a possible 12). The lowest aggregate rating for the three anterior spots in these same progenies is 5 (out of a possible 12). If the posterior spots be accepted as the best criterion of the distinction between spotless and spotted, it may be argued that there is little evidence that the spots of the spotted pattern are reduced by modifying genes, and that any beetle whose three posterior spots had an aggregate size of less than 10 should be regarded as spotless. This argument would ignore the possibility that these particular six spotted progenies merely happened to be nearly free of modifying genes. The safest assumption appears to be, however, that most of the effect of the modifying genes is exerted on the spotless gene.

An approach from the opposite direc-

tion may be made by noting the ratings of individuals which must be genotypically spotless. This can be most safely done with the parents. As a convenience in later discussions, the supposed genotypes of all parents are given in Figure 6. These genotypes are judged from the patterns of the parents, their ancestry, and their progeny. Many of the genotypes shown are certainly correct; some depend on ratios of the progeny, whether 1:0 or 3:1, and are doubtful; and a few could just as well be something else—as, for example, the parents in Experiment 112 which might about as well be *Ss* as *SS*. Some of the most certain of the genotypes will be used to judge the extent of modification of pattern.

The mother in Experiment 44 must be spotless. So also must be both parents of 48, 50, 55, 61, 62, 65, 78, 82, 84, 86, 89, 112, 133, 134, 135, 138 and 140; one or both parents of 46, 49, 56, 69, 72, 128 and 132; the fathers of 47, 74, 103 and 110; and the mothers of 52, 54 and 109. The highest aggregate size of the three posterior spots which it is necessary to assign to any spotless beetle on the basis of the above judgments is 7 (father of 56). Five others have ratings of 6, though one of these is based on descriptive records instead of an available specimen.

The highest rating of a certainly spotless beetle is thus 7, the lowest for a certainly spotted beetle is 10, for the last three spots. Since the progenies include a number of beetles between these values, it is likely that the two patterns overlap, the darkest spotless beetles being darker than the lightest spotted ones. It would be impossible, if this is true, to separate the bearers of the spotless gene in all instances from the bearers of the spotted gene. However, because the purpose of these studies is to permit a determination of the frequency of the genes from a study of the phenotypes, it would be satisfactory to establish a point at which one variety is statistically separated from the other, such that judgments of beetles near this dividing point would be as often wrong in one direction

as in the other. Let us see what basis there may be for approximating such a point.

Experiments 21, 44, 52, 54, 103 and 109 assuredly involve the mating $Ss \times ss$ or its reciprocal. Their progeny should therefore be half spotless, half spotted, if the two types are equally viable. Of these six experiments, 103 produced too few offspring to be useful, by itself, in determining what rating of the spots would divide its progeny into two equally numerous groups. In the other five the median ratings are 6, 9, 8.5, 7 and 6, respectively. If all six of the experiments be combined, the median rating of their three posterior spots is 7.2.

An independent determination of the dividing point between spotless and spotted may be made from Experiments 48, 50, 55, 62, 65, 78, 89, 133, 134, 135, 138 and 140. In all of these families it is fairly certain that both parents were Ss , and the offspring should therefore be spotless and spotted in the ratio of 3:1. If these twelve experiments be combined, it is necessary to set the dividing point between spotless and spotted at 8.2 to arrive at a 3:1 ratio.

Any compromise between the 7.2 computed from $Ss \times ss$ matings and the 8.2 from $Ss \times Ss$ matings should take into account the fact that the former value is based on 123 individuals, the latter on 266. The standard errors of the 1:1 and 3:1 ratios based on these numbers are about 7.1 and 5.5, respectively, expressed in numbers of individuals. Without further statistical refinement, which would hardly be justified, I propose to adopt the value of 7.75 as the dividing line. In practice this would require that one-fourth of the beetles rated 8 for the three posterior spots be regarded as spotless, the remaining three-fourths as spotted.

This criterion of the S and s genes may or may not be applicable to another line of descent whose modifying genes are different. In any case, it is applicable only when there is a considerable range of variation in a finely graded series. It is not applicable to a family or population in which there is a marked

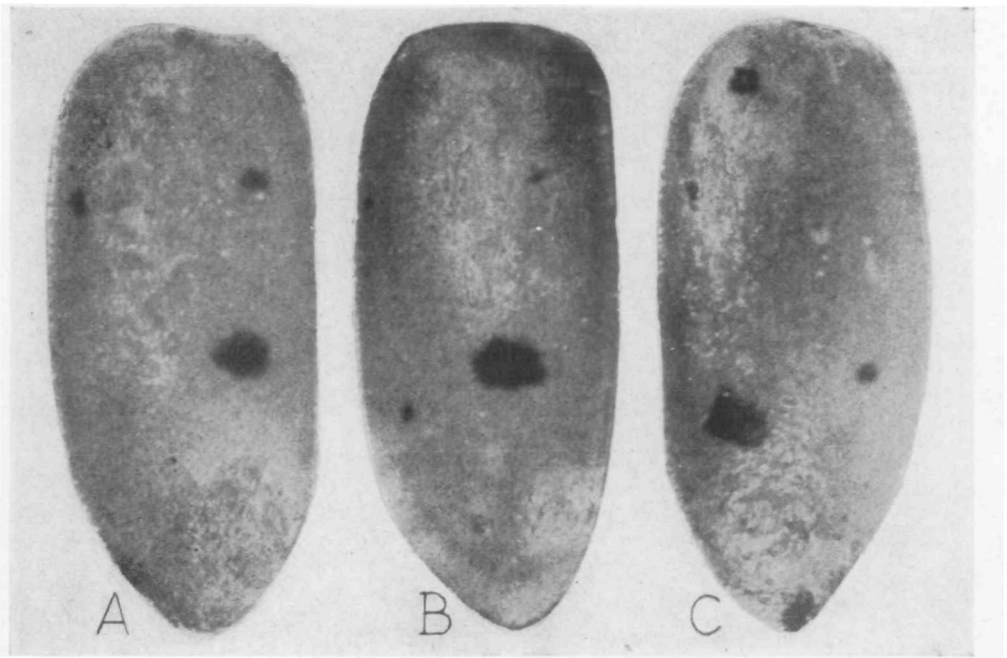
gap between a lightly spotted and a heavily spotted group, where perhaps some members of the heavily spotted group fall below the rating 8.

The Number of Modifying Genes

Any modifying genes which were possessed by the original mother of Experiment 21, and the male or males with which she mated, may have been very unequally distributed through their seven generations of descendants. It is of some importance to know the number of such genes contained in these beetles. To determine this point a standard of comparison is needed. What posterior spots could a spotless beetle have if it had no modifying genes? Experiment 82 indicates that probably it would have none, for in that experiment no individual, parent or offspring, has any of these spots. This conclusion is supported by Experiment 48, in which one parent is free of posterior spots, while the other parent has one very small one. The progeny of these parents are divided sharply into a spotless and a spotted class, with the darkest spotless beetle having each of the three posterior spots present faintly.

If complete absence of the last three spots be taken as the criterion of the absence of modifying genes, the progeny of Experiment 21 included two spotless individuals with no modifiers. The total number of spotless in this family is 21 or 22 if the above-described statistical criterion is accepted, or 16 or 17 if the family be equally divided. The spotted beetles presumably have their share of modifiers which cannot be detected in them. Thus, one-eighth to one-eleventh of the beetles have no modifiers. Assuming that the modifiers are in different pairs of chromosomes, so that they are distributed independently to the germ cells—which may not be true—one must conclude that there were three, possibly four, pairs of modifiers in the parents of Experiment 21.

No later generation has a very much smaller proportion of strictly spotless beetles (those with no posterior spots),



SPOTTED "SPOTLESS" WING COVERS

Figure 7

The dominance of the spotless gene is modified by other genes which permit some of the spots to "show through." In *A* and *B*, spot number 4 is accentuated; in *C*, spot number 5. In different parts of the range of this species different modifying genes appear to have become relatively fixed, altering the accentuation of various spots in different regions.

hence none need be supposed to have more than four pairs of modifiers. It would be easy to conceive of dominance relations which would permit an individual of a later generation to have more induced spotting than any of the progeny in Experiment 21 would be likely to have; but such an arrangement is unnecessary. Experiment 55 includes about the same proportion of unmodified spotless beetles as does Experiment 21, but most other experiments which have spotless individuals at all have more than one-sixteenth of them without posterior spots. These latter progenies must be supposed to have fewer of the modifying genes. Experiment 82 may have lost all of them, 110 and 133 all or most of them.

Qualitative Differences Among Modifiers

Whether the genes that induce spot-

ting in beetles with gene *S* are equal in their effects or whether each one affects particular spots more than others, is a question not necessarily raised in the mere determination of the number of such genes. There are some indications that the modifying genes may affect certain spots. The spotless progeny of Experiment 45 shows a strong emphasis on spot No. 4. One of the progeny of this experiment, the mother of Experiment 55 (which herself shows this emphasis on the 4-spot), together with a male from 46, which shows a smaller emphasis on spot No. 4, transmits a still observable prominence of the same spot. Another line of descent from 45 (Exps. 56 and 72), however, shows practically no accentuation of spot 4. The progeny of Experiment 52 show a similar emphasis on spot 4, derived possibly from their spotted father which would not show it. Others show a less marked in-

fluence of the same sort. See Figure 7, *A* and *B*.

The same spot (4) is, however, influenced less than the other posterior spots in some experiments, as in 61 and 89, where spot No. 5 receives the emphasis (Figure 7*C*). In none of the experiments is the sixth spot singled out for increase by the modifying genes.

Frequency of Genes in Populations

On the basis of the judgments arrived at in the foregoing experiments, several populations have been analyzed to determine from the phenotypes the frequency of gene *S* (spotless) and its modifiers. Three such populations, furnishing the original parents in the experiments recorded in Tables I and II, have been mentioned. Others have been obtained from Gold Hill, Colorado (from Prof. M. A. Palmer) and Jumbo Mountain, Colorado (from Prof. Gordon Alexander)—both of these localities relatively near Boulder; and from Sonora, California (Mr. C. E. Gustafson). I am greatly indebted to the persons named for their assistance. The largest collection from Michigan was obtained at Coloma, Michigan, through the courtesy of Mr. Tom Daggy. Numerous smaller collections come from all over the Lower Peninsula of Michigan.

The beetles in each collection have been classified as spotless and spotted. Some collections of hibernating beetles were so large that only a fraction was studied; it seemed unnecessary to classify more than about two thousand beetles from one area. The numbers of spotless and spotted from each area are recorded in the first four columns of Table III.

From these numbers has been computed the frequency (p) of the gene *S*, using the formula $p^2SS + 2p(1-p)Ss + (1-p)^2ss$ as representing the frequencies of the three genotypes. This formula rests on the assumption that those genotypes lead to equal fertility, viability and longevity, and that matings involving them are made at random. The percentage of the pertinent chromosomes which contain the gene *S*, which would also be the frequency of the gametes con-

taining that gene, is recorded in the fifth column of Table III. Gene *S* is somewhat more abundant in Colorado than in Michigan, but conspicuously less frequent in California.

The three localities in California have sufficiently different frequencies, and their geographic position is such, that a gradient is indicated. It will be of interest to obtain populations of other areas near them to discover what becomes of this gradient.

Frequency of Modifiers

Of no less interest than the distribution of the spotless gene is the frequency of its modifiers. It is clear from the relative numbers of spotless beetles having posterior spots that the several populations in Table III are not alike. A single numerical value representing the frequency of the modifying genes in each population would be desirable, but it cannot be ascertained until the genetics of these modifiers is known in some detail. Almost any set of assumptions regarding their inheritance would show the several populations to be unlike, though the nature of their differences might be incorrectly indicated. Perhaps it is worth while to use one set of assumptions.

Let it be assumed that there are modifiers of spotless at four loci (the largest number indicated by the experiments with Michigan beetles); that each modifying gene is at least partially dominant, so that a beetle heterozygous for even one of them would show some posterior spotting; and that the four modifying genes are equally abundant (which is probably incorrect). It is not necessary to stipulate that these loci be independently distributed, since in a long-time process like evolution the recombination of genes is not restricted by linkage.

To make computations from these assumptions it is easiest first to ascertain the proportion of the population which carries *no* modifying genes. This can be done only with the beetles which carry the gene *S*, since the modifiers, so far as known, have no effect on the spotted pattern. The eighth root of this propor-

tion will be the frequency of the gametes which do not carry a particular modifying gene—any one of the four, since we are postulating equal frequencies. Subtracting this root from one gives the frequency of each modifying gene.

On the basis of these assumptions, 15.73 per cent of the pertinent chromosomes of the beetles from the Lower Peninsula of Michigan should carry the first of the four genes that induce or permit posterior spots in a beetle having gene *S* (see last column of Table III). A similar number of pertinent chromosomes would contain the second of the four modifiers, and so on. Gametes, or even chromosomes, might include two or more of the modifiers.

The populations from Michigan and Colorado do not, on these assumptions, differ greatly in the number of modifiers of spotless; but the number in California is strikingly lower. Almost any set of assumptions regarding the modifying genes could hardly fail to show some kind of difference between the populations of Michigan and California.

Discussion

It is to be noted that no use of the three anterior spots of the pattern has been made in these studies. There are indications that differences in these have a genetic basis, and that variations in them may be as distinctive of geographic groups as are those of the posterior ones. They have been omitted from a first study because they are not as easy to use in an analysis of populations.

The single set of assumptions regarding modifiers of the spotless gene should not be taken as an indication that all populations are regarded as falling into the same scheme. Observation makes it highly probable that the Colorado population has other modifiers than those in Michigan. Certain combinations of emphasized spots which are frequently repeated in the former area are uncommon or absent in the latter. This must mean a difference in the modifying genes.

Attention should also be called to the fact that the rule for recognizing the spotless beetles in Michigan was in one

respect violated in its application to Colorado phenotypes. According to that rule one-fourth of the beetles which had an aggregate rating of 8 for the three posterior spots were to be regarded as spotless, the remainder as spotted. In the Colorado population the rating 8 was not infrequently attained by having two of the spots fully developed, the third one wholly lacking. The two full-sized spots might be either 4 and 5, or 5 and 6. The Michigan beetles seldom showed this type of pattern; the spotless beetles seldom had even one posterior spot fully developed, two of them practically never. It was feared that this peculiarity of the Colorado beetles is a modification of the spotted pattern, not of the spotless. Accordingly all beetles which got their rating of 8 from two large spots, with the third missing, were classified as spotted. There was no opportunity to ascertain the genetics of this pattern after it was observed.

There is little literature concerning the pattern of *Hippodamia convergens* in relation to distribution. This paucity has been mentioned in an earlier article.² Dobzhansky¹ states³ that omission of some of its spots is less common in the eastern part of the United States than in California. The studies here reported show that this difference is not the result of a lower frequency of the spotless gene in the East, for actually it is more than twice as common there as in the far West. It is caused by the modifying genes which restore to the eastern beetles some of the spots of which the spotless gene alone would deprive them.

Summary

The spotless pattern of *Hippodamia convergens* differs, in its simplest manifestation, from the spotted pattern by just one gene. The spotless gene is almost completely dominant. It may be accompanied by modifying genes which restore some, or even all, of the spots, though in reduced size. The two patterns are most sharply distinguished by the three posterior spots, but there is some overlapping even of these. In the presence of modifying genes the largest

TABLE II
Experiments with a line of descent involving modifiers of Spotless

<p>Exp. 21 111100? X spotted</p> <p>001000 122222 101000 212222 000010 123222 101110 122231 022110 101133 023110 222322 333110 444232 222020 111323 122211-2 123233 023022 332333-3 111221 444344 002122 222343 022222 444444-5</p>	<p>Exp. 49 122222 X 002122</p> <p>010000 111233 001010 123333 012010 244343 033110 233344 012111 113444 000222 322454 023222</p>	<p>Exp. 61 000000 X 001000</p> <p>000000-24 010021 100000 212121 001000-3 311121 010000 211131 101000 312131 001010 211221 101010 111132</p>	<p>Exp. 75 001310 X 110210</p> <p>000210 211332 023300 222423 011410 344344 213032 310444 122322 434444</p>	<p>Exp. 110 443444 X 000000</p> <p>000000-14 021000 010000-4 001010 011000-5 011010 110000 033010</p>
<p>Exp. 44 123222 X spotted</p> <p>111000 222044 023110 111333-3 101011 333333-2 001200 343244 101320 333344-3 202222 222444-2 222222 422444-7 222033-4 334444 111322 444444-3 222333-2</p>	<p>Exp. 50 022110 X 101110</p> <p>001000 133221 011000-4 211231 011100 032231 121100 033232 012010 220330 211010 033332 212110 322333 011200 322344 001210 434344 111210-2 444344 121210 232444 111120 421444 202120 422444 033120 423444-2 122121 441444 233220 334444 000131 244444 122221 444444-2</p>	<p>Exp. 62 301030? X 201010</p> <p>000000-2, 001220 001000 101220 101000-2 201131 011000 112131 101010-2 212131 202010 301142 100100 222233 011100 413443 200100 412344 102110 212444 301110 213444 201020 412444 101120 423444 112120 434444 111121 212453</p>	<p>Exp. 79 334344? X 433434?</p> <p>410744 422444 421344 423444-2 333344 433444-3 433344 434444 410444-2 443444-2 421444-3 444444-11 434444</p>	<p>Exp. 112 110000 X 100000</p> <p>000000</p>
<p>Exp. 45 Spotted in some X degrees</p> <p>000000-2 122212 000100 111411 101300 111333 111500-2 111222 022300 022322 000220 022333-4 011310 222333 201310 303333 220400 111444 211202 422444-5</p>	<p>Exp. 52 023110 X 334444</p> <p>011300 101233 011311 222333 021312 012433 123321 322444 023321 222444 133321 233444 211322 443444 123322 444444-1 233322</p>	<p>Exp. 65 111210 X 212110</p> <p>100000 312220 111000-3 133220 212000 213221 411110 412330 000111 311331 211111 222440 121211 311333 012210 333423 210210 413443 023300 401344 211211 422344 211220 434444-2</p>	<p>Exp. 58 000000 X 101000</p> <p>000000-26 001000-2 100000 110000 010000-5 011000-2</p>	<p>Exp. 128 344230 X 033000</p> <p>000000-2 232221 010000-2 132143 011000-3 411244 020000 421344 032000 444344-2 072000 444344-2 122021 444444 243220</p>
<p>Exp. 46 122231 X 101133</p> <p>100000-4 222220 111100 421220 001200 222320-2 011210 222333 202300 222341 100121 111333 101310 322333-2 202031 343244 220220 422444-4</p>	<p>Exp. 54 001200 X 343244</p> <p>001100 101331 201210 212232 213210 323223 011112 102332 112222 212422 113321 134233 223321 123333 011322 233434</p>	<p>Exp. 69 213210 X 223321</p> <p>111000 223310 022100 223221 122110 134321 212110 344421 112200 233333 033200 444444</p>	<p>Exp. 64 101000? X 100000</p> <p>100000</p>	<p>Exp. 132 022000 X 122133</p> <p>020223</p>
<p>Exp. 47 123233 X 023110</p> <p>011000 001333 023000 222333 011010 044333 032010 444444 023021 344454 -23121 443454 134271 444454</p>	<p>Exp. 55 201310 X 011210</p> <p>000000-2 200221 011010 011212 111100 201320 111110 321233 100200 100431 010210 111434 110210 322344 111210 322443 001310 321444 101310 222444-3 111310 411444 200211 412444-2 011122 323444 111122 422444-2 111311</p>	<p>Exp. 70 444444 X 433444</p> <p>344244 333444-2 423344 414444 434344 344444-3 444344 434444 422444 444444-5</p>	<p>Exp. 56 111000 X 000010</p> <p>000000-5 333333 001000-12 412443 010000 412444 001010 422444 201010 434454 101111</p>	<p>Exp. 133 000000-6 011000 011000-3 020011 010000-3</p>
<p>Exp. 48 001000 X 000010</p> <p>000000-5 333333 001000-12 412443 010000 412444 001010 422444 201010 434454 101111</p>	<p>Exp. 56 111323? X 022322</p> <p>011100 011233 010200-2 000234 010111 222333 011321 010433 010223 000434 011223 221444-2 010232 411444 011322 421444 010421 344444</p>	<p>Exp. 72 222333 X 010222?</p> <p>010000 122334 122134 110344 111333 421444 011334 431444</p>	<p>Exp. 66 111010? X 100000</p> <p>100000</p>	<p>Exp. 137 000000-6 011000 011000-3 020011 010000-3</p>
<p>Exp. 48 001000 X 000010</p> <p>000000-5 333333 001000-12 412443 010000 412444 001010 422444 201010 434454 101111</p>	<p>Exp. 55 201310 X 011210</p> <p>000000-2 200221 011010 011212 111100 201320 111110 321233 100200 100431 010210 111434 110210 322344 111210 322443 001310 321444 101310 222444-3 111310 411444 200211 412444-2 011122 323444 111122 422444-2 111311</p>	<p>Exp. 70 444444 X 433444</p> <p>344244 333444-2 423344 414444 434344 344444-3 444344 434444 422444 444444-5</p>	<p>Exp. 64 101000? X 100000</p> <p>100000</p>	<p>Exp. 137 000000-6 011000 011000-3 020011 010000-3</p>
<p>Exp. 48 001000 X 000010</p> <p>000000-5 333333 001000-12 412443 010000 412444 001010 422444 201010 434454 101111</p>	<p>Exp. 55 201310 X 011210</p> <p>000000-2 200221 011010 011212 111100 201320 111110 321233 100200 100431 010210 111434 110210 322344 111210 322443 001310 321444 101310 222444-3 111310 411444 200211 412444-2 011122 323444 111122 422444-2 111311</p>	<p>Exp. 70 444444 X 433444</p> <p>344244 333444-2 423344 414444 434344 344444-3 444344 434444 422444 444444-5</p>	<p>Exp. 64 101000? X 100000</p> <p>100000</p>	<p>Exp. 137 000000-6 011000 011000-3 020011 010000-3</p>
<p>Exp. 48 001000 X 000010</p> <p>000000-5 333333 001000-12 412443 010000 412444 001010 422444 201010 434454 101111</p>	<p>Exp. 55 201310 X 011210</p> <p>000000-2 200221 011010 011212 111100 201320 111110 321233 100200 100431 010210 111434 110210 322344 111210 322443 001310 321444 101310 222444-3 111310 411444 200211 412444-2 011122 323444 111122 422444-2 111311</p>	<p>Exp. 70 444444 X 433444</p> <p>344244 333444-2 423344 414444 434344 344444-3 444344 434444 422444 444444-5</p>	<p>Exp. 64 101000? X 100000</p> <p>100000</p>	<p>Exp. 137 000000-6 011000 011000-3 020011 010000-3</p>
<p>Exp. 48 001000 X 000010</p> <p>000000-5 333333 001000-12 412443 010000 412444 001010 422444 201010 434454 101111</p>	<p>Exp. 55 201310 X 011210</p> <p>000000-2 200221 011010 011212 111100 201320 111110 321233 100200 100431 010210 111434 110210 322344 111210 322443 001310 321444 101310 222444-3 111310 411444 200211 412444-2 011122 323444 111122 422444-2 111311</p>	<p>Exp. 70 444444 X 433444</p> <p>344244 333444-2 423344 414444 434344 344444-3 444344 434444 422444 444444-5</p>	<p>Exp. 64 101000? X 100000</p> <p>100000</p>	<p>Exp. 137 000000-6 011000 011000-3 020011 010000-3</p>
<p>Exp. 48 001000 X 000010</p> <p>000000-5 333333 001000-12 412443 010000 412444 001010 422444 201010 434454 101111</p>	<p>Exp. 55 201310 X 011210</p> <p>000000-2 200221 011010 011212 111100 201320 111110 321233 100200 100431 010210 111434 110210 322344 111210 322443 001310 321444 101310 222444-3 111310 411444 200211 412444-2 011122 323444 111122 422444-2 111311</p>	<p>Exp. 70 444444 X 433444</p> <p>344244 333444-2 423344 414444 434344 344444-3 444344 434444 422444 444444-5</p>	<p>Exp. 64 101000? X 100000</p> <p>100000</p>	<p>Exp. 137 000000-6 011000 011000-3 020011 010000-3</p>
<p>Exp. 48 001000 X 000010</p> <p>000000-5 333333 001000-12 412443 010000 412444 001010 422444 201010 434454 101111</p>	<p>Exp. 55 201310 X 011210</p> <p>000000-2 200221 011010 011212 111100 201320 111110 321233 100200 100431 010210 111434 110210 322344 111210 322443 001310 321444 101310 222444-3 111310 411444 200211 412444-2 011122 323444 111122 422444-2 111311</p>	<p>Exp. 70 444444 X 433444</p> <p>344244 333444-2 423344 414444 434344 344444-3 444344 434444 422444 444444-5</p>	<p>Exp. 64 101000? X 100000</p> <p>100000</p>	<p>Exp. 137 000000-6 011000 011000-3 020011 010000-3</p>
<p>Exp. 48 001000 X 000010</p> <p>000000-5 333333 001000-12 412443 010000 412444 001010 422444 201010 434454 101111</p>	<p>Exp. 55 201310 X 011210</p> <p>000000-2 200221 011010 011212 111100 201320 111110 321233 100200 100431 010210 111434 110210 322344 111210 322443 001310 321444 101310 222444-3 111310 411444 200211 412444-2 011122 323444 111122 422444-2 111311</p>	<p>Exp. 70 444444 X 433444</p> <p>344244 333444-2 423344 414444 434344 344444-3 444344 434444 422444 444444-5</p>	<p>Exp. 64 101000? X 100000</p> <p>100000</p>	<p>Exp. 137 000000-6 011000 011000-3 020011 010000-3</p>
<p>Exp. 48 001000 X 000010</p> <p>000000-5 333333 001000-12 412443 010000 412444 001010 422444 201010 434454 101111</p>	<p>Exp. 55 201310 X 011210</p> <p>000000-2 200221 011010 011212 111100 201320 111110 321233 100200 100431 010210 111434 110210 322344 111210 322443 001310 321444 101310 222444-3 111310 411444 200211 412444-2 011122 323444 111122 422444-2 111311</p>	<p>Exp. 70 444444 X 433444</p> <p>344244 333444-2 423344 414444 434344 344444-3 444344 434444 422444 444444-5</p>	<p>Exp. 64 101000? X 100000</p> <p>100000</p>	<p>Exp. 137 000000-6 011000 011000-3 020011 010000-3</p>
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<p>Exp. 48 001000 X 000010</p> <p>000000-5 333333 001000-12 412443 010000 412444 001010 422444 201010 434454 101111</p>	<p>Exp. 55 201310 X 011210</p> <p>000000-2 200221 011010 011212 111100 201320 111110 321233 100200 100431 010210 111434 110210 322344 111210 322443 001310 321444 101310 222444-3 111310 411444 200211 412444-2 011122 323444 111122 422444-2 111311</p>	<p>Exp. 70 444444 X 433444</p> <p>344244 333444-2 423344 414444 434344 344444-3 444344 434444 422444 444444-5</p>	<p>Exp. 64 101000? X 100000</p> <p>100000</p>	<p>Exp. 137 000000-6 011000 011000-3 020011 010000-3</p>
<p>Exp. 48 001000 X 000010</p> <p>000000-5 333333 001000-12 412443 010000 412444 001010 422444 201010 434454 101111</p>	<p>Exp. 55 201310 X 011210</p> <p>000000-2 200221 011010 011212 111100 201320 111110 321233 100200 100431 010210 111434 110210 322344 111210 322443 001310 321444 101310 222444-3 111310 411444 200211 412444-2 011122 323444 111122 422444-2 111311</p>	<p>Exp. 70 444444 X 433444</p> <p>344244 333444-2 423344 414444 434344 344444-3 444344 434444 422444 444444-5</p>	<p>Exp. 64 101000? X 100000</p> <p>100000</p>	<p>Exp. 137 000000-6 011000 011000-3 020011 010000-3</p>
<p>Exp. 48 001000 X 000010</p> <p>000000-5 333333 001000-12 412443 010000 412444 001010 422444 201010 434454 101111</p>	<p>Exp. 55 201310 X 011210</p> <p>000000-2 200221 011010 011212 111100 201320 111110 321233 100200 100431 010210 111434 110210 322344 111210 322443 001310 321444 101310 222444-3 1113</p>			

posterior spots of a "spotless" beetle may be larger than the smallest posterior spots of a spotted beetle. For statistical purposes, the two patterns may be separated in instances of overlapping at the point where the posterior spots have about 65 per cent of their maximum size.

Analysis of natural populations indicates that the spotless gene is present in 6 or 7 per cent of the pertinent chromosomes in Colorado and Michigan, but only in 2 to 3.5 per cent in California.

The modifying genes appear to have no effect on the spotted pattern. From the frequency of spotless beetles which have no posterior spots, and which are assumed to have no modifiers, it is computed that three or four pairs of modifying genes have been involved in one experiment. Some of the descendants of these experimental beetles certainly had fewer than four pairs, some probably none at all. The modifying genes appear to be unequal, one of them relating more especially to spot No. 4, another to No. 5.

On the basis of certain assumptions an estimate of the frequency of the modifying genes has been made. The estimates indicate that the modifiers are nearly three times as frequent in Colorado and Michigan as in California.

Literature Cited

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2. SHULL, A. F. *Jour. Hered.* 34:329-337. 1943.

TABLE I
Experiments showing inheritance of spotless and spotted patterns in *Hippodamia convergens*

Origin	Exp. No.	Ancestry of Parents		Nature of Parents		Offspring	
		♂	♀	♂	♀	Spotless	Spotted
Am. other	70	Wild	Wild	Spotless	Spotted	21	12
	77	F ₁ of 20	F ₁ of 20	Spotless	Spotless	12	7
	78	F ₁ of 20	F ₁ of 20	Spotless	Spotless	11	4
	79	F ₁ of 20	F ₁ of 20	Spotless	Spotless	11	19
	84	F ₁ of 20	F ₁ of 20	Spotted	Spotted	0	73
Pineville	264	Wild	Wild	Spotless	Spotless	24	9
	265	Wild	Wild	Spotted	Spotted	0	15
	266	F ₁ of 264	F ₁ of 265	Spotless	Spotted	19	0
	268	F ₁ of 264	F ₁ of 265	Spotless	Spotted	14	0
	270	F ₁ of 264	F ₁ of 265	Spotless	Spotted	17	0
	267	F ₁ of 266	F ₁ of 268	Spotted	Spotless	9	0
	269	F ₁ of 266	F ₁ of 268	Spotted	Spotless	15	0
	271	F ₁ of 266	F ₁ of 268	Spotted	Spotless	14	0
	272	F ₁ of 266	F ₁ of 268	Spotted	Spotless	13	0
	273	F ₁ of 266	F ₁ of 268	Spotted	Spotless	11	6
Extracted	307	F ₁ of 299	Wild	Spotless	Spotless	6	5
	319	F ₁ of 307	Wild	Spotless	Spotted	14	13
	320	F ₁ of 307	Wild	Spotless	Spotted	12	9
	324	F ₁ of 320	Wild	Spotless	Spotted	17	21
	325	F ₁ of 319	Wild	Spotless	Spotted	11	18
	322	F ₁ of 319	Wild	Spotted	Spotted	7	20
	323	F ₁ of 319	Wild	Spotted	Spotted	7	20
	326	F ₁ of 320	Wild	Spotted	Spotted	7	26
127	F ₁ of 120	Wild	Spotted	Spotted	7	29	

TABLE III
Frequency of the spotless and spotted patterns, of the gene for spotless, and of the modifiers of spotless, in *Hippodamia convergens* in several localities

Locality	No. of Spotless Beetles		No. of Spotted Beetles	Percent- Age of Purified Chromo- somes with Gene S	Percent- Age Fre- quency of Four Mod- ifying Genes
	Without posteri- or spots	With posteri- or spots			
Lower Peninsula, Mich.	87	265	2678	5.24	15.71
Colma, Mich.	61	197	1808	5.45	18.43
Gold Hill, Colorado	87	277	2311	7.02	15.16
Jumbo Mountains, Colo.	34	95	231	7.06	14.91
Yosemite Valley, Calif.	91	69	2118	7.58	6.81
Sanora, Calif.	79	18	1842	2.88	4.16
Pineville, Calif.	54	23	2067	2.04	3.77

Population Pressure in Formosa

It is obvious that no population inhabiting a limited and already densely settled area, and dependent on agriculture, can reproduce indefinitely at the rate indicated by a gross reproduction rate of about 3 and a net reproduction rate of about 2. The potential growth of the Islanders of Formosa is even more rapid than is indicated by these rates, since any social or economic changes that would promise an eventual lessening of fertility would produce immediate and more rapid declines in mortality. The actual growth may be much less rapid than the gross and net rates indicate, since the collapse of order and the discontinuance of the sanitary measures imposed by the ruling Japanese caste may eliminate the minimum control of mortality achieved during the Japanese period. The war will remove Formosa from the Japanese Empire, and thus alter the particular nexus of causal factors responsible for the extraordinary growth that occurred between 1905 and 1940. The problems of the economic and demographic future of Formosa will be minor and dependent aspects of the greatest of all Asiatic problems, the future development of the economy and the population of mainland China.—*Population Index*, July, 1944.