# HIGH MUTANT GENE FREQUENCIES IN A POPULATION OF DROSOPHILA IMMIGRANS

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The biology of *Drosophila immigrans* with particular reference to the genetic structure of several populations from widely separated points in the U. S. A. formed the subject of an earlier report (Spencer 1940). It is the purpose of this communication to present data on the genetic analysis of a Western Pennsylvania population of this species in which two mutant genes were present in high frequencies. The analysis also serves as a basis for a discussion of the method of inbreeding by $F_1$ pair matings as a means of studying the genetic structure of *Drosophila* populations in regard to the recessive visible mutations carried in heterozygous form in wild flies.

## THE POPULATION SAMPLE

On September 9th, 1944, three open traps consisting of large tin cans containing over-ripe tomatoes as bait were set in an open woodland near a stream within the environs of New Wilmington, Pennsylvania, a village a few miles from the Ohio-Pennsylvania border and located in Lawrence County. On the morning of September 11th flies from these traps were collected. The catch included many flies of the species, *Drosophila immigrans*.

As pointed out in the earlier report this species, which is tropical or sub-tropical in origin, is a highly successful introduced form throughout the U. S. A. It is more tolerant of low temperatures than *Drosophila hydei*, *melanogaster* and *simulans*, but is probably killed off outdoors in the latitude where the collection was made during severe winters. The peak populations of *D. immigrans* are found in the northeastern part of the U. S. A. in the autumn, at which time small over-wintering foci have bred up to a maximum, feeding on rotting tomatoes and other vegetables, windfall fruit and garbage. The species may be taken in woodland areas at considerable distances from human habitations during the autumn but certainly larger populations are found in gardens and orchards than in the woods.

In the village where the sample was collected *D. immigrans* was observed in great abundance in tomato patches and on windfall fruit. It seems likely that the flies taken were recent migrants from surrounding gardens and orchards. The abundance of the autumn population was not necessarily correlated with the size of the over-wintering focus from which it came, but rather with favorable conditions of temperature, moisture and food supply during the summer and particularly in late summer and early autumn. In some years and areas *D. immigrans* may be scarce even in autumn and it has been the author's experience from many collecting records that the distribution of the species from year to year and place to place is much spottier than that of *D. melanogaster*.

## THE $F_1$ GENERATION

Fifty-six pair matings of flies from the collection were made up in three-fourths ounce cream bottles containing the usual cornmeal, molasses, agar medium heavily enriched with brewer's yeast. To supply larvae with optimum conditions for feeding and pupating a modification of the method described by Spencer (1943) was used. After six days the parent flies were removed from the creamers and one-third of a double sheet of kleenex paper, soaked in a suspension of baker's yeast in water, was added to each creamer. Larvae burrow readily through the paper, find an abundant yeast supply for feeding, and an optimum place for pupa-

tion at the surface of the mat of paper. *D. immigrans* is a fly at least three times the size of *D. melanogaster*. With the technique used, in 24 cultures chosen at random from the total there emerged 1659 ♂♂ and 1632 ♀♀, an average of 133 flies per creamer. Furthermore, these flies were of uniform and normal size, and showed no evidence of overcrowding in the larval stage. The method of culture is recorded as it seems important in population studies to provide optimum culture conditions in small containers which are easily handled and occupy a minimum of space.

Out of the 56 pair matings 55 produced offspring. The flies from 24 of these cultures were carefully examined under the binocular microscope for visible abnormalities and all of these tabulated. In 20 of the 24 cultures one or more of the flies showed small extra sections of wing-vein near the distal end of the second longitudinal vein. 73 ♂♂ out of 1659 examined and 89 ♀♀ out of 1632 showed this character. In 4 of the cultures the character did not appear in the $F_1$. In 6 to 8 $F_1$ pair matings made up from each of these 4 cultures the character failed to appear in the $F_2$ flies from two of these cultures but did show in a few $F_2$ flies from the other two. This character has been found repeatedly in other populations of *D. immigrans*, and several more extreme net-venation mutants have been recov-

TABLE I

DORSO-CENTRAL BRISTLE COUNTS ON OFFSPRING OF 24 PAIR MATINGS OF WILD *Drosophila immigrans* FROM NEW WILMINGTON, PA.

Total males, 1,659; total females, 1,632. An equal or greater asymmetry in extra bristles would occur by chance less than once in 100 times.

| | EXTRA DORSO-CENTRALS | | | | |
|---|---|---|---|---|---|
| | Left | Right | Both | Total Left | Total Right |
| Males | 81 | 56 | 36 | 117 | 92 |
| Females | 185 | 138 | 111 | 296 | 249 |
| Total | 266 | 194 | 147 | 413 | 341 |

ered. It seems evident that extra-venation is a species-specific variant in *D. immigrans*. Wild flies of the species frequently show slight extra-venation and even more of them carry genetic factors capable of forming net-veins when made homozygous or acted on by modifiers.

An even more common variant among $F_1$ flies was the presence of extra dorso-central bristles. 23 of the 24 $F_1$ cultures showed this character, but in very different proportions. Table I gives a summary of the incidence of the character among the $F_1$ flies from the 24 cultures. The character appears more frequently and is more strongly expressed in females. Among the flies examined the character showed a definite asymmetry, appearing on the left side significantly more often than on the right. Tests and counts in later generations were not made and no explanation of this peculiar asymmetry was found. Like "extra-veins" this character is often met with in *D. immigrans* populations. While extra dorso-central bristles are not uncommon among wild flies of certain other species of *Drosophila*, for example *D. melanogaster* (see Dubinin, Romashov, Heptner and Demidova 1937), they are even more frequent in *D. immigrans*. It is clear that "extra dorso-centrals" has an inherited basis, and several loci may be involved. However, it is possible to find strains of this species in which the character is virtually absent.

Both "extra-veins" and "extra dorso-centrals" would seem to be species-specific variants in *D. immigrans*, highly variable in expression, found in many populations and in large numbers of flies, and probably subject to the action of genetic modifiers. Populations of this species not containing these variants are apparently more rare than those which carry them.

Among the $F_1$ flies of pair mating (26) there appeared many individuals showing stubble bristles. As all $P_1$ flies had been examined when pair matings of them were made and none had shown this character distinctly it seemed likely that both of the parents of culture (26) had been heterozygous for "stubble." This would indicate a high frequency of the stubble gene in the population, which was subsequently proved by further analysis.

### THE $F_2$ GENERATION

From the offspring of each of the 55 $P_1$ pairs of flies either 7 or 8 $F_1$ pair matings were made up, using the same culturing technique as described above. Where one of a pair of flies mated together carries a recessive visible gene in heterozygous form half of the $F_1$ offspring should carry this visible gene but none should show the character. The mating may be represented as VV x Vv, where (v) is the gene for the recessive visible and (V) its dominant allele. The offspring will be VV and Vv in approximately equal numbers. The chance then of an $F_1$ pair mating being of the favorable type, Vv x Vv, to produce some (vv) flies showing the visible phenotype in the $F_2$ will be $.5 \times .5 = .25$. The chance of a pair mating not being favorable will therefore be $1 - .25 = .75$. When two $F_1$ pair matings are made up the chance of neither of them showing the character in the $F^2$ flies will be $.75^2$ and the chance of at least one of them showing it will be $1 - .75^2 = .437$. The more $F_1$ pair matings made up the more chance there will be of recovering the visible character among the $F_2$ offspring of at least one of them.

Table II gives the results of the inbreeding test. Only the first 7 $F_2$ cultures are recorded even where 8 were reared. Of the 55 $P_1$ matings only those from which visible mutations were recovered are listed in the first vertical column to the left. The first $F_1$ matings form the second vertical column, the second $F_1$ matings the third vertical column, etc. Whenever a mutant was recovered from an $F_1$ mating it is recorded in the table.

The total number of mutants recorded in each vertical column is found at the bottom of the table. Some investigators have held that the subjective error involved in recovering visibles from a population is so great that data on visibles will be very inaccurate. Tables such as the one shown make possible an objective test of this error. Since the same mutant will often turn up repeatedly in several of the $F_2$ cultures, if the mutant is found in one of the early pair mating cultures examined it will not likely be missed in later ones where it is present. However, if the investigator is overlooking mutants in the early cultures examined he may still see them in the later cultures. Such errors would then tend to give more mutants recovered in the last cultures examined than in the first ones. Since the summary at the bottom of Table II indicates as many mutants recovered from the first three vertical columns as from the last three this error was not present. It should be remembered that 25% of the flies in a given culture are on Mendelian expectation homozygous for the mutant when both parents are heterozygotes. Even where mutant types have lowered viability or incomplete penetrance several to many flies out of the 100 or more flies in the culture will show the character. It is of course true that some mutants will have such a low penetrance and/or viability that they may be missed. Others will require special environmental or genetic tools for their demonstration. Obviously the mutants recovered represent only a fraction of the total genetic changes in the population. But for comparative purposes there is a large class of visibles which may be dealt with objectively with relatively

## TABLE II

ANALYSIS OF 55 $P_1$ PAIRS OF *D. immigrans* FROM NEW WILMINGTON, PA., BY 7 $F_1$ PAIR MATINGS EACH.

Mutants appearing in $F_2$ cultures shown.
Only numbered $P_1$ pairs from which mutants were recovered tabulated.

| $P_1$ | $F_1$-1 | $F_1$-2 | $F_1$-3 | $F_1$-4 | $F_1$-5 | $F_1$-6 | $F_1$-7 |
|---|---|---|---|---|---|---|---|
| 2 | — | — | — | brick | — | — | — |
| 4 | — | — | cveinless | — | — | brick | — |
| 5 | minute | — | stubble | — | minute | — | — |
| 6 | — | — | — | stubble | — | — | stubble |
| 9 | — | brick | — | — | — | — | — |
| 15 | — | dubonnet | — | — | stubble | — | — |
| 17 | — | — | brick | — | brick | — | — |
| 18 | — | — | stubble | stubble | — | — | stubble |
| 19 | brick | brick | — | — | — | — | — |
| 21 | — | — | — | — | — | stubble | — |
| 22 | — | stubble | brick | stubble | — | — | — |
| 24 | — | — | — | stubble | stubble | — | — |
| (26) | stubble | — | stubble | (stubble) | stubble | — | — |
| 28 | — | — | — | — | sepia-spineless | — | — |
| 29 | — | brick | — | — | — | — | — |
| 30 | stubble | stubble | — | — | — | — | — |
| 32 | broken | stubble | broken stubble | broken | — | broken | purple-net-short |
| 33 | — | — | — | — | stubble | stubble | — |
| 34 | — | — | tiny | — | — | tiny | tiny |
| 35 | — | — | — | — | — | — | stubble |
| 36 | — | dubonnet | — | — | — | dubonnet | — |
| 38 | — | — | — | — | brick | — | — |
| 40 | stubble | — | — | — | stubble | — | stubble |
| 42 | double | — | — | double | — | double | — |
| 43 | — | — | stubble | — | stubble | — | stubble |
| 46 | 2-brist. | 2-brist. stubble short-5 | — | stubble | 2-brist. short-5 | short-5 | short-5 |
| 47 | — | stubble | — | — | — | stubble | — |
| 48 | — | — | small | — | — | — | — |
| 51 | stubble | — | — | purplish-thin-sing. | — | stubble | stubble |
| 52 | — | stubble | stubble | — | — | — | — |
| Total | 9 | 13 | 12 | 10 | 12 | 10 | 9 |

NOTE: Both parents of $P_1$ (26) were heterozygous for stubble. Both parents of $F_1$ 26-4 were homozygous stubble.

small error under good culture conditions and in the hands of a competent observer.

In Table III the percentages of visibles which should be recovered out of the total visibles present in a given sample where one to five $F_1$ pair matings are reared are given. The table also shows the number of mutants actually observed and those expected in the sample analyzed. It will be seen that 36 mutants were recovered in the first 5 $F_1$ pair matings from the 55 $P_1$ pairs. This, as shown by the table, should be 76.3% of all those present. As the observed and expected frequencies for 1–4 pair matings indicate the validity of the method it is possible to estimate that there were about 47 visibles of the kind being studied actually present in the sample. When 7 pair matings are reared 87% of the total number of mutations should be found. Thus 11% or about 5 of the 47 mutations should be recorded for the first time in columns 6 and 7. Actually 4 mutations do appear here for the first time and we may assume that the 7 not found at all were present in the sample. On the average not quite one visible mutant in heterozygous form was carried per pair of flies tested. These data indicate that the total number of visibles of the kind being studied can be accurately estimated for a population sample by the method of rearing one or more $F_2$ cultures from $F_1$ pair matings of the wild pairs of flies constituting the sample.

TABLE III

OBSERVED AND EXPECTED NUMBERS OF MUTATIONS RECOVERED BY REARING 1, 2, 3, 4, AND 5 $F_1$ PAIR MATING CULTURES OF 55 PAIRS OF WILD *Drosophila immigrans*.
(See text for full explanation.)

| $F_1$ PRS. | EXPECTED PER CENT OF MUTATIONS RECOVERED | NOS. OF MUTATIONS RECOVERED | |
|---|---|---|---|
| | | Expected | Observed |
| 1 | 25% | 11.8 | 9 |
| 2 | 43.7% | 20.6 | 19 |
| 3 | 57.8% | 27.3 | 28 |
| 4 | 68.4% | 32.2 | 32 |
| 5 | 76.3% | 36.0 | 36 |

TABLE IV

A LIST OF THE DIFFERENT MUTATIONS FOUND IN THE NEW WILMINGTON SAMPLE. ALL AUTOSOMAL RECESSIVES; STUBBLE INCOMPLETE RECESSIVE.

Eye colors
(1) brick
(2) dubonnet
Wing veins
(3) broken
(4) cross-veinless
(5) short—5
Bristle changes
(6) double
(7) minute
(8) small
(9) stubble
(10) tiny
(11) two-bristle
Phenotypic Complexes
(12) purple eye—net wings—short wings
(13) purplish eye—thin bristles—singed hairs
(14) sepia eye—spineless bristles

DESCRIPTIONS OF MUTATIONS FOUND

A list of the mutations found is given in Table IV. For comparative purposes a short description of each mutation is given below. As most of the stocks were

soon discarded no symbols have been assigned to the mutations. Similarity between any phenotype and that of a mutation previously recorded in this species is mentioned. The reader is referred to Table II and descriptions of mutations in a former publication (Spencer 1940).

EYE COLORS—

(1) Brick. Austomal recessive. A dark reddish brown eye-color easily distinguished from the vermilion-like wild-type at all ages. Excellent viability. Recovered 8 times.

(2) Dubonnet. Autosomal recessive. A purplish eye-color completely separable from wild-type but only under proper lighting conditions. Good viability; female sterile. Recovered twice.

WING VENATION—

(3) Broken. Autosomal recessive. Breaks in second, third, and fourth longitudinal veins. Wings may be spread. Some hairs removed lateral to dorso-central bristles. Variable expression with normal overlaps.

(4) Cross-veinless. Autosomal recessive. Anterior cross-vein always missing; posterior cross-vein missing or broken. Developmental period lengthened several days at 22 C. Fair viability and fertility.

(5) Short-5. Autosomal recessive. Distal end of fifth longitudinal vein missing. Second longitudinal may be short and posterior cross-vein broken. Variable with normal overlaps.

BRISTLES—

(6) Double. Autosomal recessive. Two or three bristles from one basal ring. Sometimes only one small bristle or none from basal ring. Most often affects anterior scutellars, then posterior scutellars and dorso-centrals. Apparently reduplication and loss are diverse phenotypic manifestations of the spreading of bristle forming material. A similar case is reported in the phenotypic expression of the mutant, engrailed, in *D. hydei* (Spencer 1942).

(7)) Minute. Autosomal recessive. Bristles about two-thirds normal length and correspondingly reduced in thickness. Good viability. Less extreme than minute from Camp Rincon, Southern California.

(8) Small. Autosomal recessive. Bristles about three-fourths normal length. Developmental period of flies lengthened.

(9) Stubble. Autosomal, incomplete recessive. All bristles short and heavy as in Stubble of *D. melanogaster* (Bridges and Brehme 1944). Slight effect in heterozygotes. Homozygotes easily separable from heterozygotes Excellent fertility and viability. Similar to stubby from Woods Hole, Massachusetts and stubby-like from Gatlinburg, Tennessee. Recovered 19 times.

(10) Tiny. Autosomal recessive. Bristles similar to (8) above, but entirely sex-limited to male.

(11) Two-bristle. Autosomal recessive. Anterior dorso-centrals missing. A few normal overlaps.

PHENOTYPIC COMPLEXES—

(12) Purple-net-short. Autosomal recessive. Purple eye; plexus of veins around posterior cross-vein or posterior cross-vein missing; wings short. This complex semi-lethal and sterile.

(13) Purplish-thin-singed. Autosomal recessive. Dark purple eye; short, thin bristles; hairs singed and sparse; legs misshapen. This complex semi-lethal and sterile.

(14) Sepia-spineless. Autosomal recessive. Sepia eye; bristles very small, some missing; flies soon die. This complex semi-lethal and sterile.

## GENE FREQUENCY OF "STUBBLE" AND "BRICK"

The most interesting fact discovered in the course of this analysis was the high frequency of the gene, "stubble," in the sample and therefore presumably in the population from which the sample was drawn. "Stubble," a non species-specific character was recovered 17 times in the first 5 $F_2$ cultures of the $P_1$ matings. As 76% of the mutants present in the sample are recovered by 5 $F_1$ pair matings, then "stubble" was present in about 22 of the 110 flies analyzed or in 20% of these flies. As each fly carries two genes at the stubble locus this gives "stubble" a gene frequency of 10% in the sample and presumably in the population. This is a higher frequency for a given gene, either visible or lethal, than any hitherto reported for any population of any species of *Drosophila* yet investigated, excepting of course species-specific characters widespread in all or most populations of a species. Over 50 populations from the species *D. melanogaster, pseudoobscura, subobscura, phalerata, transversa, hydei, robusta, immigrans* and perhaps a few others have been studied on as large or a larger scale than the population under consideration.

The variety of structure revealed by these several populations would lead to the prediction that in a population of populations some might be found with specific gene frequencies as high as that reported here. While the samples have often been inadequate to give an accurate picture of low gene frequencies at specific loci they have been sufficiently large to reveal such a high frequency as here found if it had been present.

It becomes of interest to consider the possibilities of population structure, ecology and selection pressure which might account for the present case. One may consider the possibility that heterozygous "stubble," which has a slight phenotypic effect on bristles, actually maintained a selective advantage in the 1944 summer population of *D. immigrans* in the New Wilmington environment. Some might argue that a laboratory experiment could answer this question. This position fails to take into account the fact that it is next to impossible to simulate a natural environment in laboratory culture, particularly when that environment contains many unknown variables. Even in the relatively controlled environment of the greenhouse economic entomologists have often found it extremely difficult to furnish environmental complexes sufficiently similar to transplant successfully a greenhouse pest thriving at one place to a new environment. It is possible that a selective advantage of heterozygous "stubble" was present under the particular summer environment to which the New Wilmington, 1944, population was subjected. An approximate equilibrium of 10% "stubble" to 90% wild-type might conceivably have been reached in this particular environment by early September, 1944. It seems likely that the change in conditions from the warm, relatively dry summer to the cold, wet autumn would upset such an equilibrium before or soon after it became established. The author considers that the postulated selective advantage of "stubble" is a possible explanation of the gene frequency but not a probable one.

It might be argued that the sample represented the immediate offspring of a very few flies one or more of which were heterozygous for "stubble." As the sample was taken in a woodland lot where there were no concentrated food stores it seems unlikely that this explanation is valid. Rather it would seem that the sample represented for the most part migrants from surrounding orchards and gardens. It is quite possible that these sub-populations from which the sample was drawn would have shown large fluctuations in the incidence of "stubble." We may then assume that the surrounding population contained a 10% frequency of "stubble" or that one or more of the sub-populations contained a considerably higher percentage.

Without postulating a selective advantage of heterozygous "stubble" we may

find a valid explanation in the population structure of *D. immigrans* in this latitude. Spring collection records indicate that this species is winter-killed outdoors in this latitude at least in some winters. The population of a village will then pass through a sharp bottle-neck consisting of a relatively few individuals passing the winter in one or a few fruit-cellars or similar environment. Not every home harbors a winter population of *Drosophila* and the chance element in such overwintering is indicated by the species found from winter to winter. In the author's basement a few winters ago a small population of *D. funebris* survived until spring. This was the only species present. This winter a small population of *D. melanogaster* will survive if the housewife doesn't find the can of fruit, the metal top of which has rusted through. No other species is present.

After the overwintering of a few flies in some basement of a village home the bulk of a spring population may well be established from one or a few females which first reach a favorable outdoor breeding ground. The high incidence of "stubble" in this population might well have resulted from the chance concentration of the stubble gene through two or more of these winter bottlenecks. As more populations of *Drosophila* are investigated even higher gene frequencies in individual populations may be discovered. They will probably be found in populations undergoing sharp seasonal reductions.

In this connection the following case is of interest. Some years ago Dr. Harrison Stalker exposed a *Drosophila* trap, consisting of an open half-pint milk bottle containing banana mash, in a woodland park in Wooster, Ohio. The trap was brought into the laboratory after about a week and contained many *Drosophila* larvae. This group of larvae might be considered a small sub-population of *Drosophila*. When reared out the flies were mostly of the species, *D. simulans*, which has a very spotty distribution in this latitude. More remarkable was the fact that a large proportion of the flies showed a visible wing vein character, a conspicuous break in the second longitudinal vein. This turned out to be an autosomal recessive and the incidence of homozygotes indicated that they probably came from a pair of flies both heterozygous for the wing-vein gene. Thus this micro-population probably contained the mutant gene in a frequency of approximately 50%. Conceivably the 100 or more flies from this open trap might have established a local sub-population of *D. simulans* with an extremely high frequency of a specific mutant gene.

Further evidence on the small effective breeding size of the New Wilmington *D. immigrans* population is gained from the incidence of the eye-color gene "brick." This gene was recovered 7 times in the first 5 $F_1$ matings indicating its presence in the sample about 9 times or a gene frequency of about 4%. While the sample is probably inadequate to establish accurately the frequency of "brick" in the population, yet its repeated recovery is further evidence in favor of the postulated population structure. Another eye-color, "dubonnet," was found twice.

Seven of the "stubble" recurrences were tested for identity by cross-tests and all proved to be identical or indistinguishable alleles. A test of 4 of the "brick" recurrences showed them to be identical. With the distinct phenotypes of "stubble" and "brick" it was thought that the above test was sufficient to establish the allelism of the recurrences found. When genes reach this frequency in a local population they may persist for years. Thus the gene for vermilion eyes, a sex-linked recessive visible in *D. hydei*, attained a frequency of 6.5% in a sub-population of this species in Wooster, Ohio, in September, 1931 (Spencer 1932). This gene persisted in the local populations for at least 6 years.

This *D. immigrans* population represents an extreme variant in the population of *Drosophila* populations thus far investigated in regard to the high frequency of a single mutant gene. It indicates that under certain environmental conditions population structure may be such as to favor the rise to high values of specific gene frequencies. It is conceivable that "stubble" in heterozygous condition also had

a selective value under the particular environment to which the population was subjected. The genetic analysis of the population gave no information on the relative roles of selection, mutation rate, population size and migration. For a theoretcial discussion of the roles of these factors the reader is referred to the publications of Dr. Sewall Wright (1931; 1937). Based upon an ecological study of the species in the latitude in which this population was found the author considers that the breeding structure of the population, with sharp seasonal fluctuations in size, was probably the main factor in determining the frequency of the gene, "stubble," in this Western Pennsylvania population of *D. immigrans* in September, 1944.


## SUMMARY

A population sample of *Drosophila immigrans* was collected from three traps exposed in a woodland lot in the village of New Wilmington, Western Pennsylvania, in September, 1944.

From 55 pair matings of the wild flies $F_1$ cultures were reared; 24 of these were examined for variants and showed a high incidence of "extra venation" and "extra dorso-central" bristles, both of which are species-specific characters generally encountered in populations of this species.

"Extra dorso-centrals" was found more often in females and showed a marked asymmetry in both sexes.

In one $F_1$ culture "stubble" bristles, an autosomal, incomplete recessive appeared in homozygous form in many flies.

Analysis of the sample by 7 $F_1$ pair matings from each $P_1$ culture resulted in the recovery of 14 different visibles. Each of these is described.

A study of the data indicates that about 47 visible mutant genes, counting recurrences, were present in the 110 flies constituting the sample.

The gene, "stubble," on the basis of the number of times recovered, is estimated to have had a frequency of about 10% in the population sample.

The gene, "brick," was recovered 7 times and "dubonnet" twice.

As "stubble" showed a slight phenotypic effect in heterozygotes the possibility that it might have had positive selective value is considered.

Extreme reduction in population size resulting in chance fluctuation of gene frequencies is considered the probable explanation of the high incidence of "stubble."

Other cases of high gene frequencies probably due to such seasonal bottlenecks are cited.


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