THE SPREAD OF A GENE IN NATURAL CONDITIONS IN A COLONY OF THE MOTH *PANAXIA DOMINULA* L.

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(I) INTRODUCTION

THE spread of a gene in natural conditions is an event which repays detailed study since it provides an opportunity for examining evolution in progress. It has long been apparent to us that a careful watch should be kept for this occurrence and that whenever found it should, if possible, be analysed from two distinct points of view, ecological and genetic—a technique which has so far received much less attention than it deserves.

An instance of this kind has occurred in a wild population of the moth *Panaxia (Callimorpha) dominula* L. in the Oxford district, and we have been examining it from these two aspects for the last eight years. The experimental breeding is still in progress, and several more seasons must elapse before it is possible to report upon it in detail (it is briefly referred to on p. 167 of this paper), but the time has now come when an account can be given of the ecological side of the work, though we hope still to continue it.

We are grateful to Mr R. F. Bretherton who has on several occasions helped with the work of collecting, and to Mr W. H. Dowdeswell who took part with us in catching the 1939 sample; also to Mr T. C. Carter and Mr C. I. Rutherford who undertook a large part of the field-work in 1946. We are much indebted to them for their care and the very considerable time which they devoted to the collecting. Though, as will be explained on p. 155, the results for 1946 are reserved for discussion on a future occasion, the frequency

of the *medionigra* gene in that year is included in table 1 of this paper. We wish to express our thanks to Mr S. Beaufoy for his skill in taking the colour-photograph from which plate I has been made.

(2) DESCRIPTION AND HABITS OF THE MOTH

Panaxia dominula L. belongs to the family Arctiidæ. For the purpose of this paper it is necessary only to give a brief description of the insect itself and of its life-history and habits. Detailed information on these subjects may be obtained from Kettlewell (1942).

The chief food of the larva is Comfrey, *Symphytum officinale* L. ; but it also eats a number of other plants, especially Dead Nettle, *Lamium album* L., and Stinging Nettles, *Urtica dioica* L. and *U. urens* L. on which it may be reared. The imagines appear in July, and a single female usually lays between 200 and 300 eggs. They are smooth, round with a flattened base, and being unprovided with any means of attachment they are scattered, and lie, loose among the herbage.

The young larvæ begin to feed in late July or in August and hibernate when partly grown, usually in the third instar, hiding themselves in dead curled-up leaves. They begin feeding again in March and complete their growth in late May or early June. They are hairy, blackish in colour, with yellow markings on the back and sides. Kettlewell (*loc. cit.*) points out that they are dimorphic, some having a pattern of small white dots which is absent from others. The proportions of the two forms appear to differ widely in different localities, and intermediates between them are rare or absent.

Pupation takes place in a loose silken cocoon spun among rubbish on the surface of the ground, or just below the soil. In captivity emergence may be much in advance of the normal time, the perfect insects appearing even in May.

The larvæ seem to be free from parasitism by Ichneumonoidea, but the pupæ are frequently killed by the Chalcid *Pteromalus puparum*. Perhaps a more serious danger is a virus disease which may destroy large numbers of larvæ in their last instar and sometimes does much damage to laboratory stocks. However, mice are probably the greatest menace of *P. dominula* in the colony which we studied. They are very abundant in the locality and almost certainly eat a considerable proportion of the pupæ, though the larvæ must largely escape their attacks. Thus it will be seen that this species is chiefly eliminated in the late larval and the pupal stages.

The imago is rather variable in size, but on the average measures 48 mm. across the expanded wings ; see plate I, fig. 1. The ground-colour of the head, thorax and fore wings is deep bronze-green. The two pale marks on the thorax are a light yellow, and the spots on the fore wings are white, except for three which are normally yellow. These are the upper of the two basal spots, and that

immediately beyond it (that is to say, the central spot ; the one which is reduced or absent in the heterozygous variety *medionigra*, p. 148), also the narrow spot towards the base of the inner margin. The abdomen and hind wings are scarlet, marked with black as indicated in the figure.

The moth flies actively in the sunshine with a characteristic undulating flight which makes it rather difficult to catch. Often it rises to a considerable height and may be seen circling the tree-tops. It also sits on the herbage and is especially attracted by the flowers of Hemp Agrimony, *Eupatorium cannabinum* L. In warm weather it is, in general, easily disturbed when resting. Towards evening it usually becomes sedentary, though large numbers may occasionally be seen flying round the tops of certain favourite trees at that time, if the temperature be high. The insect flies little on dull wet days. It seeks shelter from rain by hiding under leaves and low-growing herbage, but even then it is not difficult to find. We have ourselves made large catches in drenching rain by crawling through the vegetation and boxing the specimens as they sit.

Hatching from the pupa usually takes place in the morning, and numbers of males assemble to each virgin female, attracted by her scent, and dance up and down in the air in her immediate neighbour-hood before one of them finds her. It is probable that the females almost always copulate on the day of their emergence, indeed we have repeatedly seen them doing so before their wings were dry ; they begin to lay their eggs soon afterwards. Kettlewell (*loc. cit.*) concludes, we think correctly, that the females do not fly until they have laid a considerable proportion of their eggs, which they probably do within the first twenty-four hours after fertilisation. On the whole, it seems unlikely that the females fly until the day after they have emerged, and consequently that they always scatter a large number of their eggs round the plants on which they themselves had fed. However, it will be shown (pp. 159-62) that the average life of the individual can be estimated as 6·25 days, so that the proportion of the two sexes does not greatly differ from equality among the specimens which are active, whether readily disturbed or caught upon the wing.

When the moths fly they show their scarlet hind wings and display a typical " warning coloration " ; but the pattern of the fore wings makes them rather inconspicuous at rest, particularly on a flower head. We have occasionally seen the imagines pursued and caught by birds, rather more often by dragon-flies, but neither event seems common. We ourselves do not find them unpleasant to eat, though it could always be maintained that they are distasteful to predators ; certainly they may be less palatable than other food as easily, or more easily, secured. Some specimens are unwilling to fly after capture, or when they have spent some time in the dark. If touched, they will then display the scarlet hind wings and produce two large drops of clear fluid from the front of the prothorax, just behind the

head.   It would be interesting to investigate the glands which give rise to this substance.   To us its flavour is bland, certainly not repellent.

The chief habitats of the moth are river banks and inland marshes, though it is found in one quite exceptional locality on the coast of Kent.   In such situations it usually forms localised colonies, often widely separated from one another.   Within them the insects may be very abundant, though they seldom stray beyond their confines.   In Britain the species is limited to England, where it is found from Kent to South Devon.   Its main area of distribution lies south of the Thames, though it has been taken as far north as Staffordshire.

(3) THE DRY SANDFORD COLONY

The colony which forms the subject of this investigation is situated near the villages of Dry Sandford and Cothill in Berkshire, about five miles from the city of Oxford.   It occupies a marsh the nature
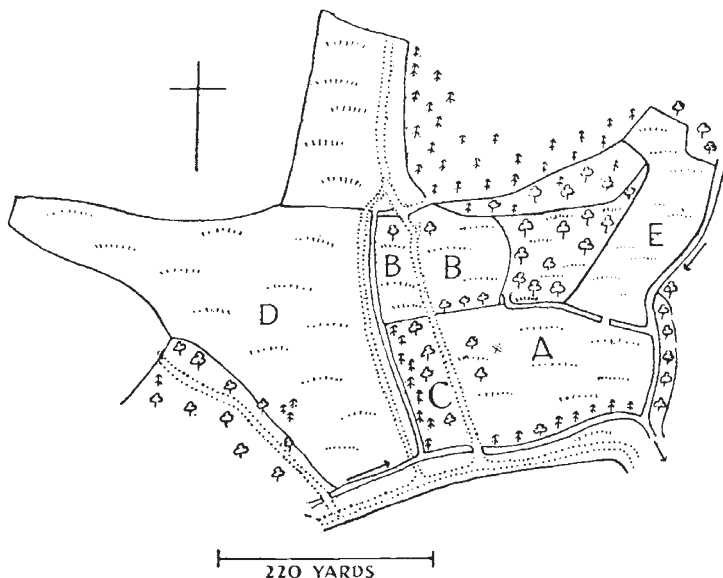

FIG. I.—Map of the marsh at Dry Sandford, Berkshire.

The colony of *Panaxia dominula* occupies the areas A. to E.   The species is most abundant in the western section of A and throughout B, also among the trees and in the open spaces in C up to the Conifers.   Specimens are also to be found sparingly along the eastern border of D, only occasionally straying to the middle of it.   They are rather scarce in area E.

The villages of Dry Sandford and Cothill lie respectively close to the east and the south sides of the marsh.   Except where other indications are given, the site is bounded by agricultural land.

* = releasing point (in area A).

of which is exceptional in that district, in some ways resembling the fens (fig. 1).   This has formed in a shallow basin partly fringed with woods.   Some of the area is occupied with birch scrub, and a

narrow belt of pines traverses it on ground which is drier than the rest. The remainder of the site is that colonised by *Panaxia dominula*, and this comprises in all about 20 acres. One portion has perhaps always been fen, and bears traces of ancient peat cuttings (Clapham and Clapham, 1939). The rest has reverted to marsh land after attempts at former cultivation, so that the remains of hedges sub-divide it. This non-wooded region falls into two types from the point of view of vegetation, and both are favoured by *P. dominula*. One part is relatively open and bears coarse grass in large hummocks, which are a great barrier to rapid progress. It is invaded to a varying extent by bushes of alder and birch. The other consists of a dense jungle of reed, *Phragmites communis*, shoulder high and more in July, together with plants of *Symphytum* and *Eupatorium* which are found in the more open ground as well. The *Symphytum* is common also along the banks of several ditches which intersect the site and drain into two small streams which border it.

The Dry Sandford area is surrounded on all sides by woods or agricultural land totally unsuited to *Panaxia dominula*, which is strictly confined to the marsh. Only two other localities for the moth have been reported in the Oxford district. One of these, where it is now appar-ently extinct, was situated at Tubney about 1½ miles away. Very few specimens from this colony exist in collections, and it is not known whether it had the special characteristics of that at Dry Sandford. Owing to the nature of the intervening country, the passage of stray specimens from one colony to the other must have been a rare event, but indeed it would not have affected the results of the present work. The remaining colony to which reference has been made is near Weston-on-the-Green, Oxfordshire. This is about 13 miles from Dry Sandford, with the city of Oxford lying between.

The evidence is rather strong that these are the only colonies of the moth in the district. The entomology of the country surrounding Oxford is as well known as any in the Kingdom. It has been worked by generations of undergraduates collecting Lepidoptera, and there have been several resident entomologists in the city throughout the present century, and long before. *Panaxia dominula*, a large day-flying Arctiid with scarlet hind wings, is among the most conspicuous of all British moths. Moreover, it is sufficiently local to be an object of much interest to the collector, and it is hardly credible that other colonies of it should exist close to Oxford without being known. Similarly, were specimens from Dry Sandford frequently to leave the marsh and stray over the surrounding country, contrary to their well-known habits, the fact would almost certainly have been dis-covered, by others if not by ourselves.

It is clear, therefore, that this colony is an isolated one ; a conclusion which receives some support from the fact that var. *medionigra* (p. 148), which in 1945 occupied 11·8 per cent. of the population there, is unknown elsewhere. This, however, is but poor

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evidence of isolation, since mutation to the gene concerned is doubtless occurring throughout the whole species, at the low rate consistent with particulate inheritance, and its absence in other colonies is probably due to its elimination there, conditions being unfavourable for it except at Dry Sandford.

(4) THE SPREAD OF THE *MEDIONIGRA* GENE

Two varieties of *Panaxia dominula* are recorded only from the Dry Sandford colony, and they must be of great rarity elsewhere. These are *medionigra* Cockayne (1928), the frequency of which has varied between 7·9 and 20·5 per cent. of the population during the period 1939 to 1946 inclusive, and *bimacula* Cockayne (*ibid.*), which is much rarer. They have now been bred extensively by several entomologists including ourselves, and it has been shown that they represent the heterozygous and homozygous expression of the same gene.

The homozygote, *bimacula*, is illustrated on plate I, figs. 7 and 8. It will be seen that it differs from the typical form (plate I, fig. 1) in a great extension of the black pigment. This replaces the scarlet on the hind wings to a considerable degree and obscures all the spots on the fore wings except the two basal ones and that on the inner margin. These three marks must be under a different genetic control for they are not reduced at all, though they may disappear in other varieties. The small white dots within the outer margin are present in some specimens of *bimacula*, absent from others. It should be noticed that the pale spots on the fore wings are replaced by black, not by an extension of the dark metallic green ground-colour ; their position can therefore be determined by careful inspection.

The heterozygotes seem always distinguishable as var. *medionigra* (plate I, figs. 3-6) in wild material, but they resemble the typical form more closely than *bimacula*. As is general, and indeed to be anticipated, in genetic studies, the rare homozygote is more variable than the common one and the heterozygote is more variable still. Typically, *medionigra* differs from the normal form in the absence of the central (yellow) spot on the fore wings, and in the presence of an additional black spot near the centre of the hind wings. Both these characters are subject to much variation. The central spot on the fore wings may be present though reduced in size, but occasionally it is as large as in the ordinary homozygous *dominula*. Sometimes also the extra spot on the hind wings may be reduced to a few black scales surrounded by a small area of yellow ones which serve to indicate its existence more clearly. Now and then, on the other hand, it is so large as to become confluent with the black spot above and below it. Plate I, figs. 3 and 4 represent the less extreme, and plate I, figs. 5 and 6 the more extreme forms of var. *medionigra*.

Collecting in Dry Sandford during 1936 and 1938, when *P. dominula* was on the wing, we noticed several specimens of *medionigra*, and it

occurred to us that the variety was more frequent than it had been in 1921, when we found no examples of it though the moth was common. The circumstance appeared to be of sufficient interest to warrant further examination, and received some support from a cursory survey of some old local collections.

These indications lead us to study the situation more thoroughly. In the first place, we endeavoured to determine the frequency of *medionigra* in former years, but it was difficult to obtain a sufficient number of specimens for the purpose. We, of course, took account only of those which were dated,* and many of these were merely labelled " Oxford " or " Oxford District." Owing to the existence of the two other localities in the neighbourhood, to which reference has been made, such insects were useless for our purpose ; we had to reject all those whose data did not specifically state that they were caught at Dry Sandford or Cothill, being the two villages bordering our locality. We examined a considerable number of collections in private hands, and in museums, in which specimens of *P. dominula* from Dry Sandford were likely to be preserved, and some contained short sets of them. It chanced that none of the insects to which we had access had been caught during the period 1929-1933, and a few only were of more recent date. As a preliminary step, we therefore decided to determine the frequency of the *medionigra* gene in specimens captured up to 1928, then ten years before, and to obtain an estimate of it the following season, that of 1939, for comparison.

After much search, we were able to accumulate 168 specimens which had been caught before 1929, and only 4 (2·4 per cent.) of them were *medionigra*. The value of this evidence requires careful consideration. Variety hunting has long been one of the chief aims of those who collect Lepidoptera, in many cases to an extent disproportionate to its real interest. It is customary, therefore, for collectors to catch a short series only of typical specimens from a given locality, but to amass all the varieties that they can obtain, unless they be very common ones. Most collections of Lepidoptera, therefore, do not represent a random assortment of each species but one which much exaggerates its variability. There is certainly no tendency for collectors to reject abnormal individuals ; a fact which anyone acquainted with butterfly and moth collecting in this country will readily endorse. Thus the sample of 168 specimens captured prior to 1929, contained in ordinary collections, will tend to overestimate, certainly not to under-estimate, the frequency of var. *medionigra*.

In 1939 we secured 223 specimens. These were a random sample in the sense that we took every individual we could catch, irrespective of form or condition. The species was unusually common that year,

* Together with some undated specimens from the colony which were known to have reached museums in bequests received prior to 1929.

and this total was obtained by three of us working throughout a single day. The moths were kept in boxes until evening, when all were released except for a few which were required for collections. There was no possibility, therefore, of counting a specimen twice. The catch comprised 184 typical *dominula*, 37 *medionigra* and 2 *bimacula*. The heterozygotes thus occupied 16·6 per cent. of the population, and the gene-frequency was 9·2 per cent., being 7·7 times greater than in the earlier sample in which, if anything, it would be exaggerated. There can be no doubt that this represents a genuine increase, and that the gene had spread in nature. Consequently, it seemed worth while to obtain an estimate of its frequency in each succeeding year.

The moth has not again been so common as it was in 1939, and from then, until 1946, only one or occasionally two people have been available for the work of collecting. Consequently, it has been impossible to catch our sample on a single day ; nor would this have been practicable when we began estimating the population numbers from 1941 onwards. In order to ensure that the same individual should not be counted again if caught on a subsequent occasion, each specimen taken was marked with cellulose paint (see p. 151 for the details of this technique). The results of this work are given in table 1, and they

TABLE 1

The distribution of the medionigra *gene among specimens caught up to 1928 and among those caught from 1939 to 1946*

Year	*dominula*	*medionigra* (heterozygotes)	*bimacula*	Total	Gene-frequency (%)
Up to 1928	164	4 (2·4%)	...	168	1·2
1939	184	37 (16·6%)	2	223	9·2
1940	92	24 (20·5%)	1	117	11·1
1941	400	59 (12·8%)	2	461	6·8
1942	183	22 (10·7%)	...	205	5·4
1943	239	30 (11·2%)	...	269	5·6
1944	452	43 (8·7%)	1	496	4·5
1945	326	44 (11·8%)	2	372	6·5
1946	905	78 (7·9%)	3	986	4·3
1939 to 1946	2781	337 (10·8%)	11	3129	5·7

will be discussed in section 6 of this paper. It should, however, be noticed at this stage that the frequency of the *medionigra* gene had greatly increased between the old samples, taken up to 1928, and that obtained in 1939, while the increase, which of course may have been very variable, was still evident the following year. In 1941, however, the gene-frequency dropped from 11·1 to 6·8 per cent. of available loci, and has subsequently shown a tendency to fluctuate round a mean of 5·2 per cent., rather than to return to the high level attained in 1939 and 1940 (9·2 and 11·1 per cent.), or to sink back to the low figure of 1·2 per cent. observed prior to 1929.

In the total sample of 3129 caught specimens, the number of *bimacula* corresponds closely with expectation based upon the number of heterozygotes (10·24 expected, 11 observed), so that our data do not of themselves suggest a differential viability between the two varieties.   On the other hand, this is inherently possible, while the error involved is great when so few *bimacula* are expected and a considerable differential viability could exist without becoming apparent in our captures.   Indeed we believe that *bimacula* is distinctly less active than the other two forms, an impression which Dr H. B. D. Kettlewell, who has an extensive experience of this insect, is prepared to endorse.   It is quite probable, therefore, that in this colony the heterozygotes are at an advantage compared with either homozygote, a situation which must necessarily lead to polymorphism.

As will be explained, we have decided not to undertake the full discussion of the last sample, that of 1946, in this paper.   However, we have included the gene-frequency of *medionigra* for that year to indicate that, though it is by a small margin the lowest since we began to study the colony in 1939, there is no evidence that in 1946 it differs materially from its values in the previous five years.

(5) THE POPULATION NUMBERS

After taking the 1940 samples, it had become clear that a situation of sufficient interest had developed to warrant estimating year by year the absolute numbers of the population in which the *medionigra* gene was spreading.   Accordingly we began this work in 1941 and have continued it each season since, using the method of marking, release and recapture, developed by Dowdeswell, Fisher and Ford (1940).   That paper should be consulted for fuller details of the technique, which are only given here in brief.

The specimens are each placed in separate boxes when caught, and at the end of the day's collecting they are marked with cellulose paint.   This has the property of very rapid drying and seals the scales on to the wing membrane.   It is then permanent and water-proof.   A dot applied with a sharpened stick is sufficiently hard in about ten seconds for the insect to be returned to its box.   Only the upperside of the fore wings is marked, for this can be seen without disturbing the insect when at rest.   Moreover, the hind wings are the more easily damaged, and a spot of paint placed upon them might be smeared if not quite dry, since they are folded and are overlapped by the front pair.   The colour of the paint and its position on the wings, left or right, basal or distal, indicates the date.   We used four colours : red (this colour being absent from the fore wings), bright green, pale blue and, when necessary, purple, and we found them easily distinguishable without risk of confusion.   A number of marks can be applied to a single insect, so that it carries a dated record of its first capture and of any subsequent recaptures.   One of the

marked specimens used in our work is shown on plate I, fig. 2. The three spots of paint on the fore wings, differing in colour and position, each indicate a date of capture and release.

The majority of the specimens sit quietly while they are being marked, for even those which were active when caught tend to become quiet after spending some time in the dark. A certain number, however, are very lively, and their wings have to be held lightly but firmly with a pair of forceps when the paint is applied and while it dries. This can generally be done without injury, but occasional specimens were damaged in the process. These were always killed ; a fact which could be taken fully into account in the records and calculations. It would of course have introduced an error to return damaged specimens to the population. For the same reason, injured or deformed specimens which were sometimes found sitting on the herbage, were not released.

The validity of our technique depends upon the free distribution of marked specimens throughout the colony, in the sense that the chances of recapturing specimens bearing a certain date-mark must be proportional to their frequency in the population at the time of recapture. This we endeavoured to secure in the following manner.

The marked insects were all taken to a central releasing point and there liberated. But, as already mentioned, we returned to the population only such specimens as appeared capable of distributing themselves freely among it, and we allowed them an adequate opportunity for doing so. If a sample were taken on successive days, work was not restarted until the insects had been flying freely for several hours since the previous release.

Marked specimens were in fact caught at the furthest limits of the colony in all directions from the releasing point even on the next day. The rather wild erratic flight of this species seems to make it but little influenced by the direction of the wind. Yet there can be no doubt that we obtained relatively more marked examples close to than far distant from the releasing point. Therefore we randomised our own captures as far as possible, spending approximately equal periods of time each day that samples were taken catching in various parts of the colony.

We also gave careful consideration to the possibility that some marked insects might have been injured without our noticing the fact, and were for this or any other reason (including what, for want of a better term, might be called a psychological one) incapable of distributing themselves throughout the colony. Accordingly, when released, the insects were thrown well up into the air, when the great majority, even of those previously sitting, would begin to fly as they fell and would be seen to scatter widely. A few, however, came down near at hand. There was good reason to think that some at least of such specimens would become active later (p. 165), so that it seemed best to make the following arbitrary decision in regard to capturing

methods.   That is to say, no collecting was done within a radius of ten yards from the releasing point.   This area was, however, carefully examined at the beginning of the work on each occasion, and marked specimens, usually only one or two, were sometimes, but not always, found within it.   These were not counted among the recaptures, and if on throwing into the air again they still fell within the ten yards radius, they were killed and entered in the table as if they had been destroyed at the time of release.

The results of this work are presented in the triangular tables (tables 2 to 6).   These are arranged like a trellis.   The dates form a horizontal row along the top, and from each of them lines descend forwards and backwards at 45° so as to interesect.   The total captured
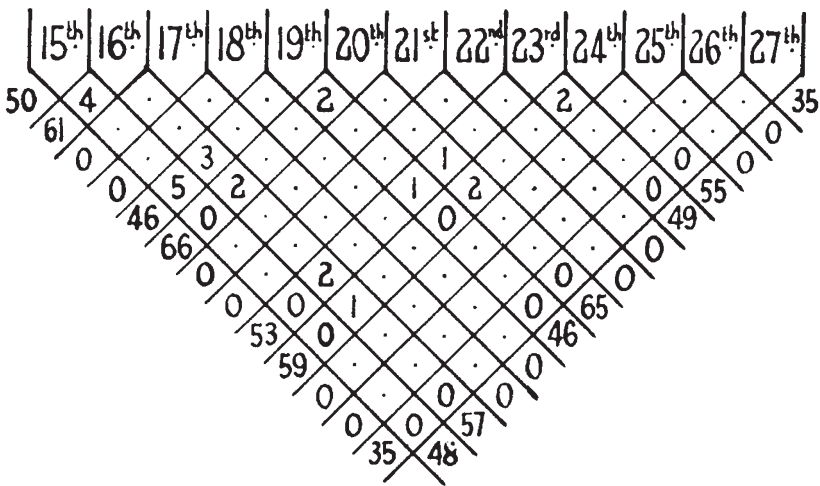

TABLE 2.—Captures, releases and recaptures of *P. dominula* in 1941.

on a given day is entered at the end of the line running south-west from the date in question, and the total released is entered at the end of that running south-east.   The number released may equal that captured or it may be less for, as previously mentioned, a few specimens may be damaged in the marking, while some may be required for other purposes and not returned to the population.   The recaptures are entered in the body of the table.   The figure o indicates that no specimens marked on a given previous date had been recaptured on a certain subsequent date.   A dot (.) shows that a recapture was impossible on the occasion indicated, either because no insects were being caught that day or because none had been released on the previous date in question.

Consider, for example, table 4 for 1943.   About the middle will be seen the entry 5.   This means that of 46 specimens released on the 14th July, 5 were recaptured on the 18th among a sample of 50, of which 48 were then released.   It will also be seen that though 47

TABLE 3.—Captures, releases and recaptures of *P. dominula* in 1942.

were released on the 15th, none of them was retaken among the sample of 29 obtained on the 19th. The row of dots passing downwards in both directions from the 17th shows that no collecting was done on that date.

The detailed analysis of these tables may now be described, but we have decided in the present paper to carry this only up to the end of 1945. The work upon the population numbers for 1946 will require further study which would hold back the present report unduly, while it is already evident that it will not substantially alter our present findings. We hope to acquire additional data for a few more years and to publish such further results, together with the findings for 1946, at a later period.
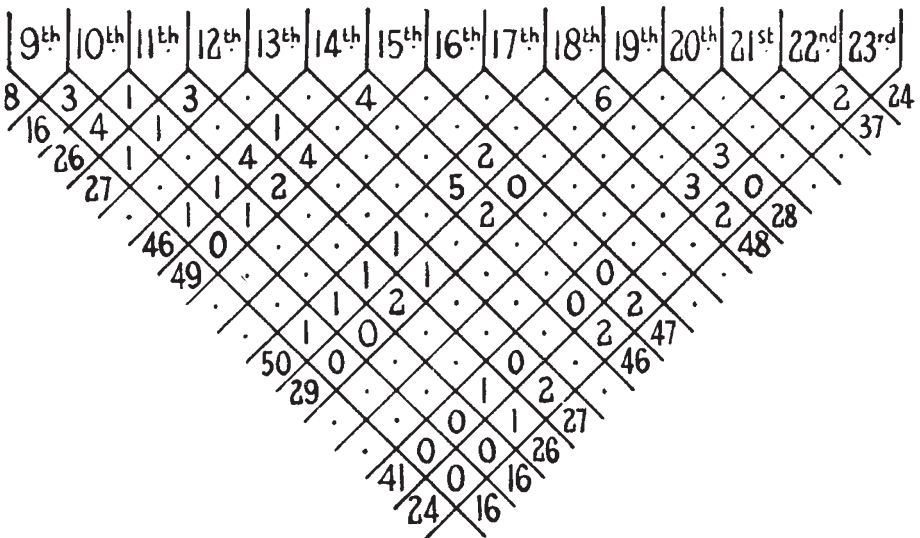
TABLE 4.—Captures, releases and recaptures of *P. dominula* in 1943.

The trellis diagrams described above give a complete account of the observational data in respect of releases, captures and recaptures, with the reservation that when, as occasionally happens, the same individual is recaptured more than once its identity, though recognised in the original record, cannot be reconstructed from these diagrams. This is a point of small importance, since not only are such individuals few, but the additional information could only be utilised in conjunction with knowledge of the manner in which the death-rate in the wild population changes with increase of age, and such knowledge we do not possess. Although it is probable *a priori* that there is some increase in the rate of elimination with increasing age from the time of emergence, the adoption of any other table of mortality than that provided by a constant death-rate is almost completely precluded by the fact that the insects are of unknown age at the time of their first capture and release. Moreover, as will be shown, expectations

based upon a constant death-rate are, in fact, somewhat closely verified in the data for the first five years (table 13), showing that in the portion of the life-span most influential upon the actual fre-

TABLE 5.—Captures, releases and recaptures of *P. dominula* in 1944.

quencies observed, the death-rate has, in fact, been sufficiently constant for our purpose. On this basis the average death-rate actually experienced by the wild populations in these years may be estimated from the average time interval which separates release

from later observed recapture. It has been found, as the following tables (especially table 13) demonstrate, that the observed difference in the distribution of time interval for these five years agrees somewhat closely with expectation on the basis of a daily elimination of 16 per cent. from the population available for capture. This corresponds with an expectation of life of $6\frac{1}{4}$ days, a value entirely consonant with experience of the moths in captivity.

11th	12th	13th	14th	15th	16th	17th	18th	19th	20th	21st	22nd	23rd
68							2					
	3							2				
	73							1				
			0							85		
				2						105		
		51	0			0			51			
		106										
			85	1				69				
					60							
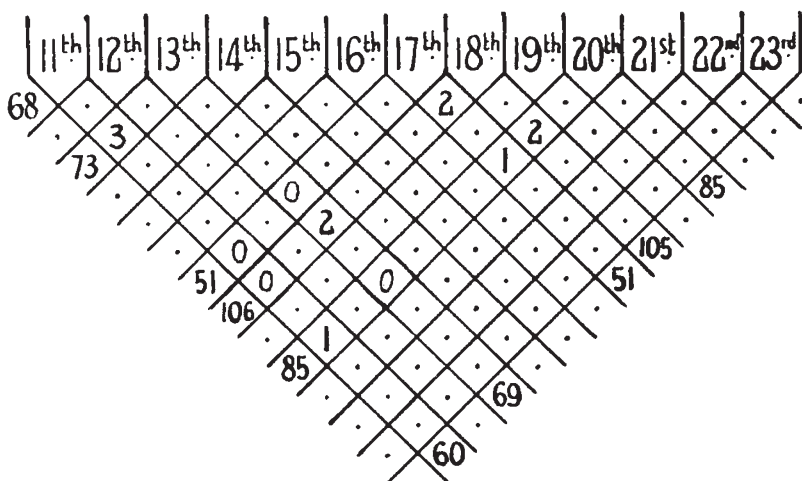
TABLE 6.—Captures, releases and recaptures of *P. dominula* in 1945.

Since the calculations are of a type which have not, we believe, been previously used or exhibited, it will be necessary to explain them at some length, and to show the arithmetical procedure in detail (tables 7 to 11). In the record for 1941, for example, captures and releases were made on seven occasions, of which the earliest was the 15th and the latest the 27th of July. There is thus the possibility of recapture at intervals from one to twelve days. The dates of release are shown in the left-hand column, followed by a column showing the days' interval from the date of release to 27th July. If this is r days, the proportion of moths released which at the survival rate adopted would survive until 27th July is $(\cdot 84)^r$. This fraction multiplied by the number actually marked and released on the six previous occasions supplies the numbers in the third column, and at any intermediate date, *e.g.* s days, before 27th July the numbers expected to be available for capture will be the sum of these entries for releases prior to that date, divided by $(\cdot 84)^s$.

Consequently, in the fourth column the entries are progressive sums from the bottom of the table, and these values divided by $(\cdot 84)^s$ give the estimated numbers of marked insects flying at any date. In this reckoning it may be noted that any insect already marked twice will be counted twice, so that if it is in fact recaptured it should be counted as so many recaptures as it bears marks.

Daily survival 84 *per cent.*

TABLE 7

1941

July	r	Released. r^t			Total recaptures	Total days survived	Excess over expectation	Total captures	Estimated number	July
26	1	...	101·87554	584·06462	0	0	0	35	∞	27
25	2	...	101·87554	482·18908	...	...	...	...	...	...
24	3	32·59872	101·87554	380·31354	...	...	...	...	...	...
23	4	24·39570	69·27682	278·43800	5	18	−2·010	59	1379·2	24
22	5	...	44·88112	209·16118	4	21	2·359	53	1194·4	23
21	6	...	44·88112	164·28006	...	...	...	...	...	...
20	7	19·18087	44·88112	119·39894	...	...	...	...	...	...
19	8	11·40229	25·70025	74·51782	4	10	−1·598	66	1437·0	20
18	9	...	14·29796	48·81757	8	29	1·686	46	331·7	19
17	10	...	14·29796	34·51961	...	...	...	...	...	...
16	11	8·37427	14·29796	20·22165	...	...	...	...	...	...
15	12	5·92369	5·92369	5·92369	4	4	0	61	614·9	16
							0·437			

TABLE 8

1942

July	r	Released. r^t			Total recaptures	Total days survived	Excess over expectation	Total captures	Estimated number	July
25	1	15·12000	51·84136	266·75526	0	0	0	9	∞	26
24	2		36·72136	214·91390	2	4	−7·705	18	393·4	25
23	3	15·41030	36·72136	178·19254	...	...	...	...	...	...
22	4	...	21·31106	141·47118	1	8	1·362	26	934·8	23
21	5		21·31106	120·16012	...	...	...	...	...	...
20	6	8·07985	21·31106	98·84906	...	...	...	...	...	...
19	7	3·24599	13·23121	77·53800	2	6	−5·720	26	489·6	20
18	8	...	9·98522	64·30679	2	12	−0·880	16	270·7	19
17	9	...	9·98522	54·32157	...	...	...	...	...	...
16	10	...	9·98522	44·33635	...	...	...	...	...	...
15	11	4·55443	9·98552	34·35113	...	...	...	...	...	...
14	12	...	5·43079	24·36591	2	10	1·027	31	573·0	15
13	13	1·76230	5·43079	18·93512	1	7	3·487	4	176·0	14
12	14	·78370	3·66849	13·50433	3	3	−8·044	17	200·5	13
11	15	1·17033	2·88479	9·83584	0	0	...	9	∞	12
10	16	...	1·71446	6·95105	0	0	...	18	∞	11
9	17	...	1·71446	5·23659	...	...	...	...	...	...
8	18	·65031	1·71446	3·52213	...	...	...	...	...	...
7	19	·80118	1·06415	1·80767	3	3	−2·096	16	130·9	8
6	20	...	·26297	·74352	1	2	−0·827	23	166·1	7
5	21	·15418	·26297	·48055	...	...	...	...	...	...
4	22	...	·10879	·21758	0	0	...	7	∞	5
3	23	·10879	·10879	·10879	...	...	...	...	...	...
							−19·396			

We shall, however, also be interested in the time intervals between marking and recapture. Column five shows the values of column four summed a second time from the bottom, so that after an interval of t days every marked insect is counted t times, thus allowing of the estimate of the total number of days between marking and recapture to be expected among those recaptured at any given date. For example, on 24th July the average number of days between marking and recapture at that date is expected to be $\dfrac{278 \cdot 43800}{69 \cdot 27682}$, and this multiplied by the number of actual recaptures on that date, namely five, gives an expectation of 20·010, which may be compared with the actual total number of days for these insects, namely 18. The excess over expectation, in this case −2·010, is shown in the eighth column.

To make an estimate of the numbers flying at any date we may multiply the expected numbers marked in the population by the total number of captures, and divide by the number of recaptures at that date. We thus obtain the estimates shown in the tenth column, corresponding to each date of collection subsequent to the first. The rows of the table are redated in the last column, since the numbers captured at any date have references only to releases at previous dates, while those released on the same day have references only to subsequent dates. The fact that these numbers are estimates, obtained by calculation, and not counts, has been emphasised by retaining one place of decimals.

The estimated rate of elimination, 16 per cent. daily, has been arrived at by making the observed discrepancy between the total days survived, and that expected, vanish approximately over the whole period of five years. The comparison is made in table 12. For three years the totals agree closely, but it may be noticed that survival is below expectation in 1942, and in excess in 1943. The former was a year of prolonged emergence and unfavourable weather, while in the latter, though total numbers are still low, the weather was favourable, and the period of emergence somewhat short. That 1943 was a favourable year is also indicated by the great increase in numbers observed in 1944 (table 15).

On occasions in which no marked moth was captured, the method of calculation described gives an infinite estimate of the numbers available. This happens frequently on the last day of the record, when the numbers available for capture have usually been much diminished, and sporadically whenever it has been impossible to catch more than a few moths. In view of the stability of the other entries we do not think these cases will cause any misapprehension. It is, however, a puzzling feature of our experience that the estimates at the later dates of collection do so often indicate the highest of the estimated numbers. For example, in 1944, numbers in the neighbourhood of 3000 are estimated for three successive days, 24th-26th July, while by 31st there were very few moths available. Apart from any

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systematic errors in the method of estimation the data would seem to imply a large increase in the death-rate towards the end of the

TABLE 9

1943

July	r	Released. r^t			Total recaptures	Total days survived	Excess over expectation	Total captures	Estimated number	July
22	1	31·08	96·54997	489·82118	11	80	24·194	24	210·7	23
21	2	...	65·46997	393·27121	7	32	−10·048	41	456·5	22
20	3	...	65·46997	327·80124	...	...	...	...	...	...
19	4	13·94040	65·46997	262·33127	...	...	...	...	...	...
18	5	20·07417	51·52957	196·86130	11	39	−3·024	29	272·9	19
17	6	...	31·45540	145·33173	11	56	5·177	50	341·9	18
16	7	...	31·45540	113·87633	...	...	...	...	...	...
15	8	11·65017	31·45540	82·42093	...	...	...	...	...	...
14	9	9·57792	19·80523	50·96553	11	29	0·693	49	355·9	15
13	10	...	10·22731	31·16030	7	23	1·673	46	322·8	14
12	11	3·96676	10·22731	20·93299	...	...	...	...	...	...
11	12	3·20867	6·26055	10·70568	5	8	−0·550	27	230·1	12
10	13	1·65863	3·05188	4·44513	5	9	1·717	26	128·6	11
9	14	1·39325	1·39325	1·39325	3	3	0	16	71·7	10
							19·832			

TABLE 10

1944

July	r	Released. r^t			Total recaptures	Total days survived	Excess over expectation	Total captures	Estimated number	July
30	1	...	98·36094	775·35552	0	0	0	9	∞	31
29	2	...	98·36094	676·99458	...	...	...	...	...	...
28	3	...	98·36094	578·63364	...	...	...	...	...	...
27	4	...	98·36094	480·27270	...	...	...	...	...	...
26	5	28·02120	98·36094	381·91176	...	...	...	...	...	...
25	6	23·53697	70·33974	283·55082	4	22	5·875	67	2817·2	26
24	7	16·22997	46·80277	213·21108	3	8	−5·667	68	3019·8	25
23	8	...	30·57280	166·40831	2	12	1·114	58	3004·5	24
22	9	9·16149	30·57280	135·83551	...	...	...	...	...	...
21	10	...	21·41131	105·26271	3	11	−3·749	46	1576·8	22
20	11	...	21·41131	83·85140	...	...	...	...	...	...
19	12	11·47716	21·41131	62·44009	...	...	...	...	...	...
18	13	...	9·93415	41·02878	5	22	1·350	98	1577·7	19
17	14	3·04774	9·93415	31·09463	...	...	...	...	...	...
16	15	...	6·88641	21·16048	2	4	−2·146	37	1463·0	17
15	16	2·70347	6·88641	14·27407	...	...	...	...	...	...
14	17	2·58058	4·18294	7·38766	7	15	2·637	47	457·1	15
13	18	...	1·60236	3·20472	3	6	0	50	517·4	14
12	19	1·60236	1·60236	1·60236	...	...	0	...	...	...
							−0·586			

season, which is in itself not improbable. Trial calculations based not on a constant expectation of life, but on one decreasing so rapidly

as a half-day for each day of survival, do not appear to make any appreciable difference to the absolute or the relative numbers estimated as flying at different dates. It would appear, therefore, that the late occurrence of the largest numbers indicated by our tables is not probably due to any systematic error ascribable to the assumption of constant death-rate.

TABLE 11

1945

July	r	Released. r^t			Total recaptures	Total days survived	Excess over expectation	Total captures	Estimated number	July
19	1	...	137·17008	493·82486	4	16	1·600	85	2914·9	20
18	2	74·08800	137·17008	356·65478	...	...	...	...	...	...
17	3	30·22790	63·08208	219·48470	4	12	1·562	106	2369·2	18
16	4	...	32·85418	156·40262	0	0	0	51	∞	17
15	5	...	32·85418	123·54844	...	...	...	...	...	...
14	6	...	32·85418	90·69426	...	...	...	...	...	...
13	7	20·36123	32·85418	57·84008	...	...	...	...	...	...
12	8	...	12·49295	24·98590	3	6	0	73	1030·2	13
11	9	12·49295	12·49295	12·49295	...	...	...	...	...	...
							3·162			

When, as on 17th July 1945, no recaptures appear in a satisfactory catch, it is easy to make a joint estimate from the data of adjacent days, such as 17th and 18th of that year, from which it appears that the estimated number 2369·2 for 18th July would be raised by the experience of 17th to 3076·0. It is thus probable that on these days the numbers were as many as, if not more than, on 20th July.

TABLE 12

	Expected	Observed	Difference
1941	81·563	82	+0·437
1942	74·396	55	−19·396
1943	259·168	239	+19·832
1944	100·596	100	−0·596
1945	30·838	34	+3·162
	546·561	550	+ 3·439

That the death-rate adopted is in agreement with our general experience over these five years is shown by table 12, which shows for each year, and for the total, the numbers expected and observed for total days survival in the wild population of marked specimens recaptured. On the total data the number observed is more favourable, but by less than 1 per cent., than the value expected. It may be

mentioned that in 1946 survival was again below expectation, as in
1942, so that had all six years been used the average mortality would
have been somewhat heavier than that which we have adopted.

A somewhat more searching comparison is also possible from
tables 7-11 ; for, knowing the approximate numbers of surviving
insects marked at each previous marking date we can calculate the
numbers of each of these to be expected among a given total number
recaptured. This enables us to reconstruct the actual numbers to be
expected among recaptures bearing marks 1, 2, 3, ... days old.
Table 13 exhibits this comparison for the total of five years' experience.
Had there been a striking increase of death-rate with age in the life
period of the insects actually affecting our record, it might be expected
that although the mean interval between marking and recapture is
brought to agreement as shown in table 12, yet that observations
should fall short of expectations at the beginning and end of table 13,
while being in excess for the middle entries. As table 13 shows,
however, there is no sign of any disturbance of this kind, the observa-
tions at all intervals from one day to the longest survivals to be
expected, *i.e.* ten days or more, showing, in fact, a striking agreement
with expectations based on the known numbers released at previous
dates.

TABLE 13

*Distribution of intervals between marking and recapture compared with
expectation on the assumption of a constant death-rate of 16 per cent. daily*

5 years, 1941-45		
Days	Expected	Observed
1	41·292	41
2	21·499	22
3	25·295	25
4	23·295	25
5	14·152	13
6	4·202	2
7	8·194	7
8	6·292	9
9	3·279	4
10	1·765	0
11	1·301	4
12 and over	2·422	1
	152·988	153

Since the date of capture of all insects is known, the records provide
material for testing whether the variant gene to which the forms
medionigra and *bimacula* are due is associated in nature with earlier
or later emergence than its normal allelomorph. Had only the two
forms *dominula* and *medionigra* occurred in the records for each year,
we should have been content to examine this point by a simple

comparison of the mean dates of (first) captures of these two forms. In several years, however, the form *bimacula* also was captured, and, although few in numbers, these specimens are particularly relevant to the question of date of emergence.   At each date of capture, in fact, we are concerned with the observed gene-ratios in the insects caught, rather than the ratio only of the two commoner genotypes. From this point of view the question is closely analogous with that of the regression of gene-ratio on date of capture, with the reservation that since we know the numbers upon which each gene-ratio is based we need not rely upon the observed day-to-day variation to supply an estimate of its precision.   The test may, in fact, be made by isolating a single degree of freedom from the observed frequencies of the three possible genotypes at all dates.

If in the record of any year the proportion of variant genes observed is p, and the date of a particular observation t, then the number of *bimacula* observed on any occasion has a coefficient $2(1-p)t$, the number of *medionigra* has similarly the coefficient $(1-2p)t$, and the number of *dominula* has the coefficient $-2pt$.   To obtain χ^2 for the one degree of freedom concerned, the square of this component is divided by $2p(1-p)\Sigma n(t-\bar{t})^2$, where n is the total number caught at any date.

The comparison between the mean dates for the (first) captures of insects bearing these two allelomorphic genes is shown in table 14 ;

<div align="center">TABLE 14</div>

	Normal gene July	Variant gene July	Difference d		χ^2	
1941	20·228	20·857	+0·629	later	3·6357	
1942	15·582	13·364	−2·218	earlier	2·3124	
1943	15·713	16·133	+0·420	later	0·2768	
1944	20·171	19·600	−0·571	earlier	0·5781	
1945	16·079	16·063	−0·016	earlier	0·0011	
1946	20·127	20·155	+0·028	later	0·0035	
					6·8076	$n=6$

the χ^2 measure of significance is shown in the last column.   It appears that of six years' experience the variant gene has been later in three and earlier in three, and that in four years out of six χ^2 is less than its average value unity.   In 1941 and 1942 there are slight indications of a difference in the date of emergence ; but these are in opposite directions, and evidently our experience gives no indication of any general association of the genes concerned with date of emergence. Nor do the data show any significant heterogeneity from year to year in this possible effect, since the total of χ^2 for six degrees of freedom comes to 6·8076, very close to its expectation.

It is, perhaps, worth little to draw attention to associations that

are not statistically significant, but it so happened in these six years that the range for the mean date of first capture is only 4·646 days for the normal gene, against 7·493 days for the *medionigra* gene. It would not be surprising if the variants were less thoroughly stabilised against environmentally induced disturbances of the date of emergence than are the typical insects.

To pass from estimates of the numbers available for collection, on days on which collection took place, to estimates of the total emergence of a whole season is a matter of some difficulty. If indeed estimates could be made every day for the whole period of about three weeks during which any of the moths are to be caught, the knowledge we have obtained of the average length of life in the field would give the total population of the year, by adding together the numbers available on each day, and dividing by 6¼. However, collecting cannot be carried out every day, and in any case no good estimates are possible until a considerable population of marked insects has been built up. In these circumstances only rough and tentative estimates are possible.

For years in which the season was quickly over, such as 1941 and 1945, there are only a few days for which the numbers are well determined. In these years, however, it is reasonable to suppose that a large proportion of those emerging in the year were alive at the time the daily numbers were at their height. Thus the total emergence must have been about 2000 to 2500 in 1941, and about 4000 in 1945. In 1942 the season was unusually prolonged, moths could be caught for at least 23 consecutive days, but all estimates were small. The maximum may not have exceeded 500 ; on the other hand, the death-rate in this year may have been exceptionally high, and although the total emergence may not have exceeded 1200, it may have been as high as 2000. In 1943, on the other hand, catches were good, but for only 14 days ; the estimates show that numbers did not rise much above 300 to 400, but were well maintained. The total emergence for this year may have been no more than 1000. Finally, in 1944, the numbers were certainly over 1000 for something like a fortnight and exceeded 3000 at the peak. The total emergence must have exceeded 5000. These imperfect estimates, the result of the comparison of numerous tentative approaches, are summarised in the following table.

TABLE 15

Approximate estimates of numbers observed

1941	.	.	.	.	2000 to 2500
1942	.	.	.	.	1200 to 2000
1943	.	.	.	.	1000
1944	.	.	.	.	5000 to 6000
1945	.	.	.	.	4000
1946	.	.	.	.	6000 to 8000

An estimate for 1946 is added. This year the moths were exceptionally abundant for fully three weeks. For most of this time, however,

less than 2000 must have been flying. On the other hand, the death-rate seems to have been somewhat high, so that the total emergence might have exceeded 8000.

Two sources of error other than those so far discussed might be thought to affect these estimates of the absolute numbers of *Panaxia dominula* in our colony.

First, it has been suggested that a significant proportion of the specimens rarely fly but remain in a semi-quiescent state sitting about on the herbage throughout their lives. This, if correct, would tend to make our estimate of the population too low, were our samples derived predominantly from insects caught on the wing. But that was not so : not only were they netted as they flew of their own accord or were disturbed, but a careful search was made for those resting on herbage or under leaves, and on wet days almost the whole of our samples had to be obtained in that way. In addition, we attacked this suggestion experimentally in the following manner during the years 1944 and 1945.

A decision was reached as to whether or not any given specimen was a potential (if not an actual) flying member of the population. In these two years all individuals found at rest were disturbed by shaking the plants on which they were sitting until they were dislodged. If they flew, they were regarded as potentially active, but if they allowed themselves simply to fall inert, they were regarded as being in a quiescent state at least for the time being and were given a distinctive mark (with cellulose paint).

During these two years, 868 unmarked specimens were caught, and 151 of them were quiescent according to this definition. In all, 40 marked specimens were recaptured, of which 36 were " active " when retaken. Yet 9 of these 36 active recaptures were marked to indicate that they had been quiescent when first found. Moreover, though 4 marked individuals were quiescent when recaptured, one of them had been " active " when it had been originally taken. Thus though a not inconsiderable proportion of the specimens (approaching one-sixth) may be found in a torpid condition, the evidence does not support the view that a significant number of them remains so permanently.

Secondly, it seems probable that females rarely fly for the first 24 hours after emergence (p. 145), and they are certainly the less active at all times. Thus they tend to be in excess among the quiescent captures, as is indicated in table 16, in which the sexes of active and quiescent specimens caught in 1945 are tabulated. Consequently, were our captures restricted to flying specimens which, as already explained, they were not, there would be a tendency to omit a proportion of the females from the calculations.

One general point of importance must be stressed in regard to these suggested sources of error. We believe we have demonstrated that they do not bias our sampling ; but even if it had not been

possible to establish this, they would still be immaterial to our purpose since they would both tend to make our estimate of the total population too small. Now it will be explained in section 6 that the crucial

TABLE 16

The numbers of active and quiescent males and females caught in 1945

	Males	Females	Total
Active	176	133	309
Quiescent . . .	28	35	63
	204	168	372

matter for our conclusions is the lower not the upper limit of the population size, in the sense that our results would be vitiated if we could not demonstrate that this colony has consisted of almost 1000 imagines each year. Provided that our estimates satisfy this require-ment, errors which tend to make them too small would only strengthen our conclusions still further. On the other hand, had these suggested sources of error acted in the opposite direction, and tended to indicate that our estimates of the total population were inflated, the validity of our deductions would have been threatened.

Field studies in the area of the Dry Sandford colony might suggest that our estimate of the total number of imagines hatching in any one year (varying between about 1000 to about 6000) is too low, for in their season the nearly full-fed larvæ are extremely abundant. It would be easy to collect 1000 in a few hours and to return the next day and obtain as many with as little trouble. As suggested on p. 144, we have strong reasons to suspect that the chief elimination in the life history of this insect occurs near the end of larval life and in the pupa. The larvæ are almost free from parasitism, nor have we found them attacked by birds. The virus disease which sometimes takes a heavy toll of this insect destroys the larvæ in their last instar, while *Pteromalus puparum*, which is a serious enemy, is purely a pupal parasite. Moreover, moles and mice are extremely common in the habitat, and they may well eat large numbers of pupæ but few, if any, larvæ. Females lay, on the average, between 200 and 300 eggs ; consequently, though our estimates suggest that during 1939 to 1945 the total number of imagines emerging in one year has not reached 6000 and has several times been little above 1000, it would not be surprising if the number of well-grown larvæ in this locality was between 50,000 and 100,000 in most of the seasons during which we have been at work.

No simple relation exists between the size of the population per season and the frequency of the *medionigra* gene. Doubtless the fact

that the population numbers are far from stable contributes to, and is itself an expression of, the changes in the direction and intensity of selection which are responsible for the variations in the proportions of the two allelomorphs (pp. 168-71) ; but it would be a situation of perhaps unexpected simplicity if the population-size and gene-frequency showed obvious correlation.

We must at least mention another aspect of our work on *Panaxia dominula*, merely to indicate that it is under investigation though we reserve it for discussion at a later date. From 1939 to 1946 the heterozygotes have on the average occupied 10·8 per cent. of the population, and even after the high value of the first two years their average frequency has been 9·9 per cent. (for 1941-46). Should such a proportion be approximately maintained, or increased, some evolutionary modification of the heterozygous phenotype might conceivably take place fast enough to be detected during a human lifetime, so providing a remarkable opportunity for observing the effects of selection upon the gene-complex of a wild population. We are here assuming the type of selective dominance modification first suggested by Fisher (1928), and this has already been successfully demonstrated in domestic animals by Fisher (1935, 1938), using poultry, and in wild material by Ford (1940) using the Currant Moth *Abraxas grossulariata*, and by Fisher and Holt (1944) using the house mouse. By means of selection experiments, carried out on the heterozygote, which is subject to considerable variability (plate I, figs. 3-6), we are now establishing the inherent possibility of discovering such an effect in the Dry Sandford colony of *Panaxia dominula*. The work is not yet complete, but in seven generations *medionigra* has become relatively more dominant in one line and more recessive in another, the difference being already significant. The variability concerned therefore appears to be of such an order as to encourage us to watch for comparable results in nature, in which case the process of evolution would have been foreshadowed in the laboratory.

(6) THE SIGNIFICANCE OF CHANGES IN GENE-RATIO

Great evolutionary importance has been attached by Sewell Wright (1931, 1932, 1935, 1940) to the fact that small shifts in the gene-ratios of all segregating factors will occur from generation to generation owing to the errors of random sampling in the process by which the gametes available in any one generation are chosen to constitute the next. Such chance deviations will, of course, be greater the smaller the isolated population concerned. Wright believes that such non-adaptive changes in gene-ratio may serve an evolutionary purpose by permitting the occurrence of genotypes harmoniously adapted to their environment in ways not yet explored, and so of opening up new evolutionary possibilities. Consequently, he claims that subdivision into isolated groups of small size is favourable to evolutionary progress, not, as others have thought, through the

variety of environmental conditions to which such colonies are exposed, but, even if the environments were the same for all, through the non-adaptive and casual changes favoured by small population size. Those evolutionists who find it difficult to attach any great evolutionary significance to such chance effects, have urged that the normal segregation of all factors in each generation continually supplies new genotypes selected at random from a number usually much greater than the number in a single generation of even a numerous population, and that the selective increase or decrease of any gene is determined by the totality of the life experience of all these, comprising as they do large numbers of harmonious, or successful, and of inharmonious, or unsuccessful, combinations : that the number of genotypes tried will generally be larger in more numerous than in less numerous populations ; and that the existence of very small and completely isolated populations, such as Wright seems to postulate, will generally be terminated by extinction in a period which must be thought of as short on an evolutionary scale of time.

There is a further possibility which, if established, would cut at the root of the whole theory, namely that populations, large and small, are subjected from generation to generation to selective intensities capable of producing greater fluctuations in gene-ratios than could be ascribed to random sampling. The data obtained on *dominula* are peculiarly well fitted to examine this possibility, since here we have in a succession of generations estimates both of a gene-ratio and of the population-size of the colony. The latter are indeed rough and of unknown precision ; but since of the six years available in only one can the population have been so small as a thousand, and as isolated colonies materially smaller than this must be in constant danger of extinction, it will be worth the while to determine whether the fluctuations in gene-ratio available for eight successive years are so small as to be reasonably ascribable to random sampling in a population of a thousand each year, or whether they show such larger fluctuations as would require the action of selection varying perhaps both in intensity and direction from year to year.

Since the gene frequencies observed vary from about 10 per cent. to less than 5 per cent., the precision of the determinations on a percentage scale would be unequal, even if the numbers of insects had been the same from year to year. For this reason it is desirable to apply the angular transformation, $p = \sin^2 \alpha$, for which the information available about the angular measure of gene frequency, α, is proportional to the number of observations. Table 17 shows the number of observations and the angular measures in degrees for the sequence of eight years.

The amount of information for any year will then be independent of α and equal to

$$\left(\frac{\pi}{90}\right)^2 n = \frac{n}{820 \cdot 7016}$$

where n is the number of observations, or twice the number of insects counted.

TABLE 17

	Number n	Angular measure a
1939	446	$17°\cdot6497$
1940	234	$19°\cdot4712$
1941	922	$15°\cdot1531$
1942	410	$13°\cdot3938$
1943	538	$13°\cdot6588$
1944	992	$12°\cdot2974$
1945	744	$14°\cdot7144$
1946	1972	$11°\cdot9108$

On the theory to be tested the measures of gene-ratio observed will be connected by a chain of random sampling processes.   Each observation, based on a random sample of $\frac{1}{2}n$ insects out of a population of $\frac{1}{2}N$, will diverge from the true value of the population by a difference the variance of which (ignoring the constant) is

$$\frac{1}{n} - \frac{1}{N};$$

while any two successive population values will have a random difference of which the variance is

$$\frac{1}{N}$$

where N is twice the number of the second population.   Consequently, choosing the population value of any year as origin we can write down the covariance matrix for samples of given size from eight successive generations.   Thus, using the population value for 1942 as origin, we should have the covariance matrix :—

$$\begin{vmatrix}
\frac{1}{n_1}+\frac{2}{N} & \frac{2}{N} & \frac{1}{N} & 0 & 0 & 0 & 0 & 0 \\
\frac{2}{N} & \frac{1}{n_2}+\frac{1}{N} & \frac{1}{N} & 0 & 0 & 0 & 0 & 0 \\
\frac{1}{N} & \frac{1}{N} & \frac{1}{n_3} & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & \frac{1}{n_4}-\frac{1}{N} & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & \frac{1}{n_5} & \frac{1}{N} & \frac{1}{N} & \frac{1}{N} \\
0 & 0 & 0 & 0 & \frac{1}{N} & \frac{1}{n_6}+\frac{1}{N} & \frac{2}{N} & \frac{2}{N} \\
0 & 0 & 0 & 0 & \frac{1}{N} & \frac{2}{N} & \frac{1}{n_7}+\frac{2}{N} & \frac{3}{N} \\
0 & 0 & 0 & 0 & \frac{1}{N} & \frac{2}{N} & \frac{3}{N} & \frac{1}{n_8}+\frac{3}{N}
\end{vmatrix}$$

Inserting in this expression the eight values of n from table 15, with N equal constantly to 2000, the arithmetical values of the covariance matrix giving the random simultaneous deviations of the eight observations from any chosen value for the 1942 population are shown in table 18. This has been simplified by inserting a factor of 10,000.

TABLE 18

Numerical values of covariance matrix

32·4215	10	5	0	0	0	0	0
10	47·7350	5	0	0	0	0	0
5	5	10·8460	10	0	0	0	0
0	0	0	19·3902	0	0	0	0
0	0	0	0	18·5874	5	5	5
0	0	0	0	5	15·0806	10	10
0	0	0	0	5	10	23·4409	15
0	0	0	0	5	10	15	20·0710

The matrix shown in table 18 is next inverted to provide the information matrix of these eight observations. This is shown in table 19, in which the factor of 10,000 has been removed. Associated

TABLE 19

Numerical values of information matrix

347·0642	−58·7863	−132·8960	0	0	0	0	0
−58·7863	230·0762	−78·9645	0	0	0	0	0
−132·8960	−78·9645	1019·6665	0	0	0	0	0
0	0	0	515·7244	0	0	0	0
0	0	0	0	599·3877	−140·6958	−32·8447	−54·6714
0	0	0	0	−140·6958	1077·2624	−208·0013	−346·2272
0	0	0	0	−32·8447	−208·0013	863·9748	−533·8740
0	0	0	0	−54·6714	−346·2272	−533·8740	1083·3411

with table 19 we have marginal totals formed by adding the entries in each row, and a second series derived from each row by multiplying each entry by the angular measure of gene frequency and adding. These two series are shown in table 20. If a_{ij} is a typical entry in the information matrix, these are

$$A_i = \sum_j a_{ij}$$

$$T_i = \sum_j a_{ij} a_j$$

The ratio of the totals from table 20 is $\bar{a} = 14°\cdot23245176$, and the heterogeneity of the observations on the hypothesis considered is found from the expression $\sum a_i T_i - \bar{a} \sum T_i$, or numerically $17207\cdot2297$. Since angles have been measured in degrees this is divided by $820\cdot7016$ to obtain the value of χ^2 for the seven degrees of freedom

among eight independent observations. We find, therefore, $\chi^2 =$ 20·8064, a value which demonstrates very significant heterogeneity, since the 1 per cent. value is only 18·475. Not once in a hundred

TABLE 20

Margin and weighted margin of information matrix

	A	T
1939	155·3819	2967·1528
1940	92·3254	2245·7422
1941	807·8060	11568·0003
1942	515·7244	6907·5095
1943	371·1758	5322·2540
1944	382·3381	4141·3336
1945	89·2548	3347·5100
1946	148·5685	43·3833
	2567·5749	36542·8859

random trials, therefore, would differences in gene-ratio so great as those observed be exhibited by observations of random samples of the sizes used, from a population of 1000 in each generation, in which reproduction was at random, and in which, therefore, changes in gene-ratio are ascribable to random survival only. Still less could they have arisen in a larger population.

The conclusion that natural populations in general, like that to which this study is devoted, are affected by selective action varying from time to time in direction and intensity, and of sufficient magnitude to cause fluctuating variation in all gene-ratios, is in good accordance with other studies of observable frequencies in wild populations.* We do not think, however, that it has been sufficiently emphasised that this fact is fatal to the theory which ascribes particular evolutionary importance to such fluctuations in gene-ratio as may occur by chance in very small isolated populations. Evidently, however large a population might be, its gene-ratios will fluctuate in the same manner and to approximately the same extent as those of the smallest isolated population which can be expected to persist in nature.

(7) SUMMARY

1. The spread of a gene in an isolated colony of the moth *Panaxia dominula* L. (family Arctiidæ) has been studied from 1939 to 1946, and compared with its frequency prior to 1929.

2. The habits of the moth and the nature of the colony are described.

3. Specimens heterozygous for the gene in question are distinguishable, as var. *medionigra*, from the other two genotypes, but they

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* For instance, considerable seasonal changes affecting gene-ratios or inversion-frequencies have been demonstrated by Dobzhansky (1943) and Timoféeff-Ressovsky (1940).

resemble more closely the normal form *dominula* than the rare homo-zygote var. *bimacula*.

4. Prior to 1929, the frequency of the *medionigra* gene in this colony was not more than 1·2 per cent. In 1939 it had reached 9·2 per cent., and in 1940 11·1 per cent. (20·5 per cent. of the population being heterozygotes). From 1941 to 1946 it has fluctuated round a mean of 5·2 per cent., showing no tendency to return to the high value of 1939-40 or to the low one observed previous to 1929.

5. From 1941 onwards, the absolute numbers of this population have been estimated by the method of marking, release and recapture, which is described. The data so obtained are recorded by means of trellis diagrams.

6. New methods have been devised for analysing these results.

7. Our findings are consistent with a constant death-rate, such that 16 per cent. of the population are eliminated daily, giving an average expectation of life of 6·25 days.

8. Tables 7 to 11 give estimates of the absolute numbers flying on each day of collecting.

9. There is no indication that in nature the forms *medionigra* and *bimacula* emerge earlier or later than the normal *dominula*.

10. Estimates have been obtained year by year for the total emergence during the whole season. This did not fall below a minimum of 1000 (in 1943) nor rise above a maximum of 6000 to 8000 (in 1946). During 1944 (total emergence 5000 to 6000) as many as 3000 moths might have been flying at the time of maximum abundance.

11. It has been suggested that two sources of error might have affected our estimates of the absolute numbers : that a significant proportion of the specimens may remain quiescent throughout their lives, and that the females rarely fly for the first 24 hours after emergence. It has been shown that such considerations do not influence our results. Moreover, both would tend to make the estimates too low ; so that they would not in any event have vitiated our conclusions, which require that the total yearly population of imagines should not fall appreciably *below* 1000.

12. A simple direct relation between population-size and the frequency of the *medionigra* gene is scarcely to be expected, and has not been found.

13. Breeding experiments conducted in the laboratory have shown that the expression of the *medionigra* gene can be modified by artificial selection. Watch is being kept for any corresponding effect in nature under the influence of natural selection. It is possible that this may be detected if the present frequency of heterozygotes in the colony is maintained or increased.

14. An angular transformation of gene-frequency, for which the information available becomes proportional to the number of observations, is used to test whether the observed yearly fluctuations

Panaxia dominula L.

FIG. 1.—Typical form, the common homozygote (*dominula*).

FIG. 2.—*Ibid.* One of the marked specimens used. The three marks, in different colours and positions, each indicate a date of capture and release.

FIGS. 3-6.—Heterozygotes (var. *medionigra* Cockayne), showing less and more extreme forms.

FIGS. 7-8.—The rare homozygote (var. *bimacula* Cockayne), showing less and more extreme forms.

in gene-ratio are small enough reasonably to be ascribed to random sampling in the reproduction of a population of 1000 each year.

15. It is, in fact, found that the observed fluctuations in gene-ratio are much greater than could be ascribed to random survival only. Fluctuations in natural selection (affecting large and small populations equally) must therefore be responsible for them. The possibility that random fluctuations in populations much smaller than 1000 could be of evolutionary importance is improbable in view of the frequency with which such small isolated populations must be terminated by extinction within periods which must be extremely short from an evolutionary point of view.

16. Thus our analysis, the first in which the relative parts played by random survival and selection in a wild population can be tested, does not support the view that chance fluctuations in gene-ratios, such as may occur in very small isolated populations, can be of any significance in evolution.

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