EVOLUTIONARY STUDIES ON *MANIOLA JURTINA*: THE ENGLISH MAINLAND, 1956-57

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1. DEVELOPMENTS IN THE AREA OF THE SOUTH ENGLISH STABILISATION

IN the years 1950-52 Dowdeswell and Ford (1952, 1953) found that throughout a large part of Southern England the females of *Maniola jurtina*, the Meadow Brown Butterfly, were so stabilised that all populations showed a characteristic spot-distribution with a large mode at 0 spots. The area in question stretched from the east coast (Ipswich), westwards to the Devon-Cornwall border, where there occurred a change within some twelve miles to another stabilisation in which the female spot-distribution is bimodal with a large mode at 0 spots and a lesser mode at 2 spots (defined as the East Cornish stabilisation). In their 1953 paper, however, they noted that at Tiverton (1951) in the extreme west of the South English stabilisation area, the female distribution showed a reduction of the steepness of the mode at 0 spots. The sample obtained at Taunton, Somerset, in 1952, had a similar tendency. With the small number of samples then available, however, these slight divergences did not much disturb the extreme and remarkable homogeneity of South English populations up to the region of the Cornish border.

By 1955 two other stabilisation areas, apart from those of South England and East Cornwall had been discovered, one in Penwith (in west Cornwall) and the other in the large islands of the Scilly group.

Sampling in the South English area was resumed in 1956 and it immediately became clear that the old stabilisation had broken up; most populations showed greatly increased spotting in both males and females, and the mode at 0 spots in the female distributions was reduced and even sometimes accompanied by a secondary mode at 2 spots—a condition which up to 1952 had only been observed in east Cornwall and a few adjacent parts of Devon.

(i) *Definitions of the South English spot-distributions*

For convenience we have named the three types of spot-distribution found in the females in 1956 and 1957 as follows :

(i) *Old English* (O.E.) : the females maintain a pattern such that the specimens at 0 spots are 60 per cent. or more of the total

of specimens at 0, 1 and 2 spots, and the specimens at 2 spots do not exceed the number of those at 1 spot.

(ii) *New English* (N.E.) : the females show a pattern in which the specimens at 0 spots are less than 60 per cent. of the total at 0, 1 and 2 spots ; the specimens at 2 spots do not exceed the total of those at 1 spot.

(iii) *Pseudo-Cornish* (P.C.) : the females show a pattern in which there is a major mode at 0 spots and a minor mode at 2 spots.

No attempt will be made here to deal in detail with the male spot-distributions. It may be briefly said that males with spot-numbers in excess of 2 were generally much more common than those with spot-numbers less than 2, and that some correlation with the three grades of female spot-frequency could be seen.

(ii) *Features of the South English data of* 1956 *and* 1957

All the data for these years are reproduced in the appendices 1 to 4. Three main trends can be observed in them :

(i) 1956 seems to have marked the peak of a wave of high-spotting which occurred simultaneously nearly everywhere in the former South English stabilisation area. The populations in that year were very large. In 1957, after an abnormally mild winter and a prolonged spring drought, the species was much rarer ; the wave of high-spotting receded, except in the south-western counties of Devon, Somerset and Dorset.

(ii) In contrast to the situation in 1950-52, there were marked differences in the spot-distributions from place to place in 1956 and 1957. In both these years, however, a strong stabilisation of " New English " populations was found in the south-western part of the area, in the counties of Devon, Somerset and Dorset. This fortunate event has enabled us to study the transition from unimodal to East Cornish bimodal distributions in great detail (see below, pp. 371-82). Figs. 1 and 2 show by means of triangular graphs the relationships of the South English samples in the two years.

(iii) A new and most remarkable feature of the post-1952 South English collections has been intra-seasonal heterogeneity. We are indebted to J. D. F. Frazer for pointing this out. He collected *M. jurtina* in the 1955, 1956 and 1957 seasons at Burham Down, Kent. (His 1955 collection is the only one known to us to have been taken on the mainland in that year.) These samples show a clear pattern in which both males and females have high spot-averages at the beginning of the emergence, but suddenly change to lower spot-averages towards the middle of the emergence. Frazer kindly sent a copy of his data to us late in the summer of 1956. In 1957 and 1958 we obtained samples

throughout the emergence at a number of localities and certain of these confirmed the Burham Down observations.

During the period of stability in 1950-52 we had obtained samples at various stages of the emergence at different localities and this had not, it seemed, in any way upset the general pattern of marked homogeneity. It occurred to us that the intra-seasonal shift, first observed by Frazer, was associated with changes in stabilisation and might indeed be one of the means by which such changes came about. This was confirmed by two opposing sets of data :

(*a*) Sampling of the Middleton (East) population throughout the 1957 emergence showed us that no intra-seasonal shift occurred there (see appendix 3). This locality is one of the two where no departure from the " Old English " stabilisation has been observed.

(*b*) Data from extensive samples of the Ipswich population, which were kindly sent to us by S. Beaufoy, show that the early emergence in 1956 was of a rather high-spotted N.E. type ; in 1957 the early emergence was similar, but was known to be succeeded by an O.E.-type later emergence ; in 1958 the whole emergence was homogeneous and conformed to the N.E. type.

In selectional terms the intra-seasonal shift suggests that in some populations an ecological factor which normally operates adversely against the high-spotted specimens was lifted simultaneously over large parts of South England during such a time of year as to disturb the balance only of the first half of the emergence ; genes for high spotting might then be perpetuated in larger numbers than usual and would then have the opportunity in some cases to percolate through all or most of the emergence next year. This seems to have happened at Ipswich, eventually producing a population stabilised on the N.E. level instead of the O.E. level observed in 1950-52. In other cases, the move towards high-spotting seems to have been unsuccessful and may have been limited to the early part of the emergence before finally disappearing. (Appendices 2 and 4 contain the data relevant to the intra-seasonal shift.)

All data given in this series of papers are the result of estimates made by at least two of the authors according to the system described in Dowdeswell and Ford (1953) ; it would therefore be improper to make direct comparisons between data resulting from scoring by another worker and our data, since slight differences in convention might occur and upset the accuracy of the estimate. We have for this reason listed Frazer's data separately, which he kindly permits us to reproduce, though it is clear that comparisons made between his estimate of spotting in the early and in the later parts of the emergence are perfectly valid.

(iii) *Geographical patterns in the former South English stabilisation area, 1956-57*

If the former South English stabilisation area is broken up into three sub-areas, (i) the south-western counties, that is, Devon, Somerset and Dorset, (ii) the south-eastern counties, that is, Hampshire, Sussex and Kent and (iii) counties lying north of the line joining the Severn and Thames estuaries, we find that populations in the south-western sub-area, with very few exceptions, have been stabilised on the New
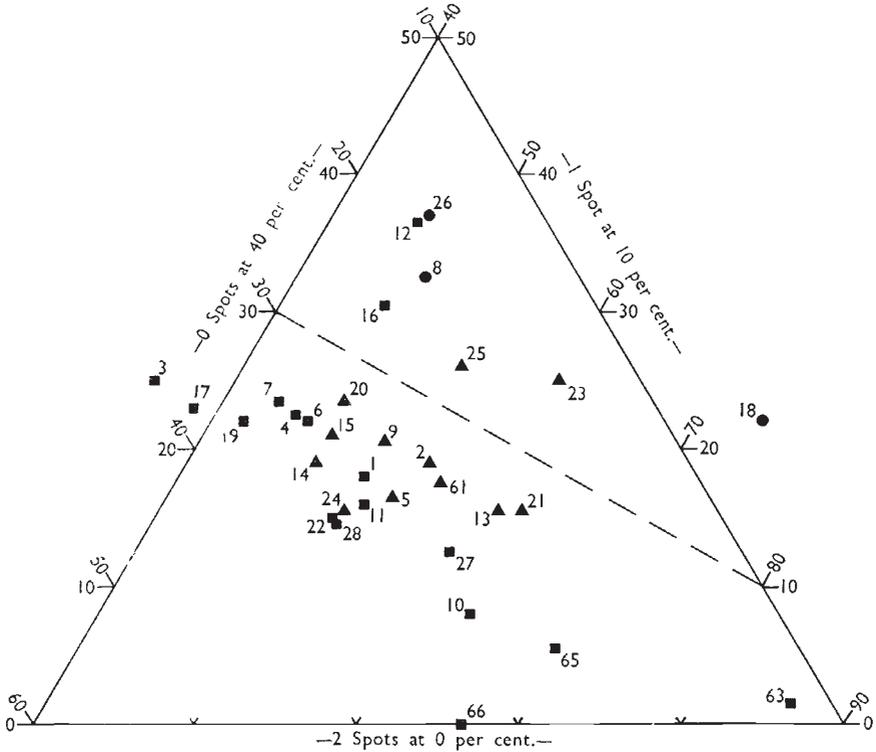

FIG. 1.—*Maniola jurtina* : English mainland and peripheral populations—female spot-distributions 1956. The frequency of 0, 1 and 2 spots are expressed as percentages of the total of these three values, the tail being disregarded. Entries above the broken line refer to bimodal samples. The numbers correspond to places listed in appendices 1 to 3 and table 1. ●—"East Cornish" populations ; ▲—the south-western sub-area, including Lundy Island ; ■—the remainder of southern England and its periphery.

English distribution since 1956, and that populations in the south-eastern sub-area showed slight differences in 1956, though not in 1957, from those of the more northerly counties.

In figs. 1 and 2, the south-western samples are represented by triangles to distinguish them from the rest of the former South English stabilisation area. The numbers following the places mentioned below refer to entries in these figs.

1956, *O.E. populations* included Middleton East (10) and, marginally, Woolbury Ring (27) in Hampshire, Sherborne (21) in Dorset and Newton Abbot (13) in Devon.

1956, *N.E. populations* included Middleton West (11), Worthy Down (28), Canterbury (1) and Shoreham (22) in the south-east sub-area ; these four maintained modes at o spots between 50 per cent. and 60 per cent. and reference to fig. 1 will show that they are somewhat distinct from the samples obtained in the more northerly sub-area, which includes Chelmsford (3), Holt (6), Ipswich (7), Rugby (19), Cothill (4) and perhaps the small sample from Oxford,
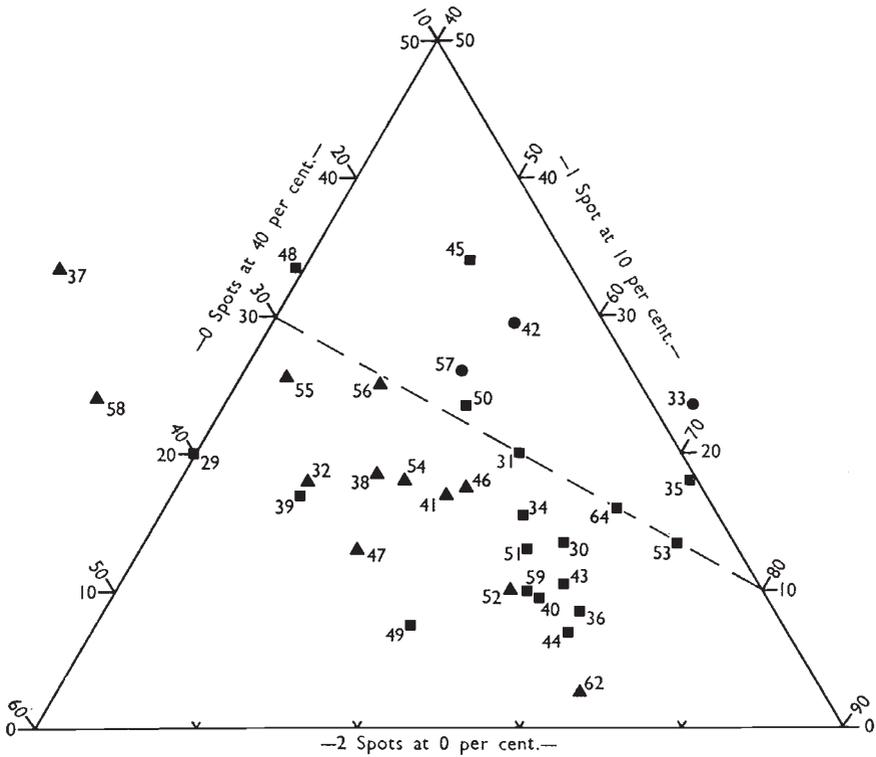
F*ig*. 2.—*Maniola jurtina* : English mainland and peripheral populations—female spot-distributions 1957. For explanation see fig. 1 on page 366.

Parks (17). The south-western sub-area was strongly stabilised, as reference to fig. 1 will show.

1956, *P.C. populations* included Oxford, Medley Manor (16), Tiverton (25), Taunton (23) and perhaps Newbury (12), where our sample was very small.

1957, *O.E. populations* included all localities in the south-eastern and northerly sub-areas, though Ipswich (39 and 40), Oxford, Medley Manor (48 and 49) and Oxford, Parks (50 and 51) only showed this distribution in the second phases of their emergences. One exceptional south-western locality, Pilistreet (52) near the border of the East Cornish stabilisation, also showed the O.E. distribution (see p. 380).

1957, *N.E. populations* included all south-western localities except Pilistreet (52) ; also the first phase of the Ipswich emergence (39).

The two outstanding western populations Newton Abbot (47) and Sherborne (54) moved over from O.E. to N.E. against the general trend.

1957, *P.C. populations* included Newbury (45) and the first phases of the two Oxford samples (48 and 50). Hoylake (35), with a large

TABLE 1

Spot-distributions of M. jurtina *populations in areas peripheral to the former South English stabilisation area*

Locality	Year		Spots						Total
			0	1	2	3	4	5	
— Lundy Island .	1955	♂	5	5	34	2	...	...	46
		♀	47	18	5	...	...	...	70
61. ,, ,, .	1956	♂	3	7	62	24	1	...	97
		♀	45	21	14	4	...	...	84
62. ,, ,, .	1957	♂	1	1	14	3	...	...	19
		♀	29	10	1	...	...	...	40
63. Isle of Man .	1956	♂	7	22	85	13	...	1	128
		♀	102	15	2	...	...	...	119
64. Pont-l'Evêque, *Normandy*	1957	♂	1	1	27	10	...	...	39
		♀	47	11	11	3	...	...	72
65. Sutherland .	1956	♂	8	27	101	19	6	...	161
		♀	73	26	6	2	...	...	107
66. Sutherland (area " D ")	1956	♂	2	18	33	2	...	...	55
		♀	10	5	...	...	...	...	15

The serial numbers in the left-hand column refer to the corresponding entry in figs. 1 and 2.

mode at 0 and a small, possibly not significant, mode at 2 spots, seems aberrant.

(iv) *Long-term behaviour of stabilisations*

It should not be thought that the events described in Southern England are unique. Although so far as our information goes the East Cornish and West Cornish (Penwith) stabilisations seem to have remained unaltered from 1952 to 1958, the fourth stabilisation known to us, that of the large islands of Scilly, after being in force from at least 1950 to 1955, began to break up in the direction of lower spotting in 1956 and had been partly restored by 1958. As in South England, one area (the largest of the islands), remained undisturbed throughout. Details of these events will be communicated in a paper devoted to the Isles of Scilly ; an account of the large island stabilisation up to 1955 is given in Dowdeswell, Ford and McWhirter (1957).

(v) *Populations in areas peripheral to the former South English stabilisation area*

We have information on the condition of *M. jurtina* in the following areas :—Lundy, 1955-57 ; Isle of Man, 1956 ; Sutherland, Scotland, 1956 ; Pont-l'Evêque, Normandy, 1957. The data are listed in table 1.

The Sutherland samples are fully discussed in Forman, Ford and McWhirter (1959). It will be noticed that the Lundy Island population tends to conform not with the south-western region (Devon, Somerset and Dorset), as might be expected from its geographical position, but with the more remote parts of Southern England. The Manx sample maintains its strong deviation towards very low spot-values in both sexes which has been observed since 1951. Our first sample from Normandy seems to conform generally to the South English stabilization.

2. THE WEST DEVON AND CORNWALL AREA

(i) *Survey of previous results* *

By the end of the 1951 season it had become clear that spotting in the females of *Maniola jurtina* was stabilised throughout the South of England with frequencies descending from a single mode at 0 spots. This pattern of frequency-distribution will be referred to as the " Southern English stabilisation ". As already explained, however, minor variants can be recognised within it (the Old English and the New English forms, with more and less pronounced modes respectively). This general type of unimodal spotting distinguished all the populations studied from the North Sea to east Devon, though they are subject to great environmental differences, of climate, soil and vegetation.

As a result of work in previous years, it had already been realised that, widespread as it is, the Southern English stabilisation breaks down to other and characteristic values in some parts at least of Cornwall (Falmouth in the south and Hayle in the north). It was therefore decided to explore the situation from east Devon westwards in 1952.

Collecting was extremely hampered by wet weather, following long-continued heat and drought which had brought out the species unusually early, before we ourselves could be in the field. Five samples from central and west Devon were obtained. Three were caught in the middle of the county, respectively at Okehampton, Lydford and Holsworthy. The others were taken near the south coast, at Newton Abbot (mid-Devon) and at Noss Mayo (five miles east of Plymouth). In all of them, the females were unimodal at 0 spots as in the rest of England eastwards, and the five populations

* The individual data upon which the results referred to in this sub-section are based can be obtained from Dowdeswell and Ford, 1953.

2 A

were homogeneous with one another ($\chi^2_{(4)} = 5\cdot39$, with P between $0\cdot3$ and $0\cdot2$).

It should here be mentioned that in 1951 an additional sample (not published in our 1953 paper) was obtained only a mile or so from Plymouth, though still to the east, in the Plymstock area (see table 2). The females are very homogeneous when compared with the samples obtained the following year in the above five Devon localities ($\chi^2_{(2)} = 0\cdot362$, with $P = 0\cdot9$ to $0\cdot8$). It will be noticed that the high mode at 0 (over 60 per cent.) is consistent with the Old English type. This is confirmed by the males, which have a large mode at 2 spots and, for what the figures are worth, approximately equal numbers above and below that value.

TABLE 2

Spot-distributions at Plymstock, 1951

	Spots					Total
	0	1	2	3	4	
Females	34	14	4	2	...	54
Males	1	3	19	2	1	26

Proceeding farther west, to the neighbourhood of the Devon-Cornwall border and east Cornwall, samples from another group of five localities (Plymouth North, Plymouth Roborough, Tavistock, Lewannick and Lanivet) were obtained in 1952. Here we pass to a situation of a different kind, in which the females are bimodal with a greater mode at 0 spots and a lesser at 2. These five populations also proved homogeneous with one another ($\chi^2_{(12)} = 8\cdot778$, with $P = 0\cdot8$-$0\cdot7$), in spite of considerable differences in habitat : coastal, inland and a locality (Lanivet) separated from the rest by the granite intrusion of Bodmin Moor. The difference between this group and the one just referred to from Devon is immensely significant ($\chi^2_{(3)} = 41\cdot481$). When the 1951 Plymstock sample is included, the distinction is increased to $\chi^2_{(3)} = 50\cdot978$.

After the 1952 season we were, then, faced with the following situation. A stability, characterised by female spotting unimodal at 0 spots, persisted from the coast of the North Sea across Southern England to west Devon. Near the Cornish border, and for a considerable distance beyond, this is replaced by a bimodal spot-distribution, also homogeneous. That area was sampled well inland (Lewannick), half-way thence to the south coast (Tavistock), at two places near Plymouth, and thirty miles westwards (Lanivet).

Although we are not in this account concerned with the situation in west Cornwall, it is desirable for completeness to mention that *Maniola jurtina* becomes rare or absent in the country immediately

east of the Hayle-Marazion isthmus, isolating an entirely distinct and apparently stabilised type on the Land's End peninsula ; one in which the females are unimodal at 2 spots like the males, only with the mode less pronounced. Two somewhat exceptional populations are left on either side of this stretch of isolating territory ; in the Falmouth district to the south and on the Hayle sandhills, in wholly abnormal conditions, to the north.

The whole situation here described is the one which Dobzhansky and Pavlovsky (1957) summarise in the following terms : " Populations of the butterfly *Maniola jurtina* are rather uniform throughout southern England, despite some obvious environmental diversity in different parts of this territory." In reality, the respective stabilisations persisted in the face of great environmental differences, while the chances (measured by $\chi^2_{(3)} = 41\cdot481$ with $P = 5\cdot17 \times 10^{-9}$) * are almost 1 in 200 million that the distinction between the Devon (*i.e.* Southern English) and East Cornish stabilisations is fortuitous. The difference is even greater when the Plymstock sample, not previously described, is included (p. 370). Considering this, and the other facts mentioned here, it seems that Dobzhansky and Pavlovsky's statement has not been based upon a sufficiently detailed examination of the published data.

(ii) *Results obtained in* 1956 †

Subsequently to 1952, work on *Maniola jurtina* in the Isles of Scilly prevented us for some years from returning to the study of this insect on the mainland. In 1956, however, we determined to examine the way in which the spot-distributions found respectively in Devon and east Cornwall change from one to the other.

As explained previously, we already knew that the difference between them is very great and that each is homogeneous over a wide and highly diversified area, coastal and inland. It was also clear that there was no tendency for the two types to approximate even in the localities we had examined where they approached most closely. In the inland sector, which was the one we selected for study (see map, fig. 3), these were twelve miles apart, at Lydford (Devon) and Lewannick (Cornwall). Provided that the diversity had persisted throughout the intervening four years, the problem was likely to be of much interest since it will be seen that at its longest the cline involved could be no more than twelve miles. Yet the facts prove more surprising than anything we had anticipated.

The work was conducted by K. G. McWhirter and E. B. Ford without W. H. Dowdeswell who, unfortunately, could not be present in 1956. Our first task was to determine whether the Devon and East Cornwall populations previously studied still remained dissimilar. We therefore visited the large field (SX634992) which had provided the

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* This extension of the χ^2 table was kindly calculated for us by Mr N. T. J. Bailey.

† A combination of letters and numbers in brackets following a locality represents its position on the National Grid.

Okehampton sample in 1952 ; also the Lydford locality (SX487863) twelve miles farther west-south-west. The results are shown in tables 3 and 4 for the two sexes separately, where they are compared with the

TABLE 3

The Devon and Cornish spot-distributions for 1952 and 1956 compared in the Okehampton to Lewannick transit ; females

Locality	Year	Spots						Totals
		0	1	2	3	4	5	
Okehampton, *Devon*	1952	36	9	5	3	...	...	53
,, ,,	1956	45	29	20	5	...	...	99
Lydford, *Devon*	1952	21	12	3	...	...	...	36
,, ,,	1956	50	27	20	11	...	...	108
Lewannick, *Cornwall*	1952	28	17	21	7	...	...	73
,, ,	1956	44	18	30	10	2	...	104

1952 data when available. It is evident that the females are still clearly unimodal at 0. This mode is, however, somewhat less accentuated, and to a significant degree. The difference between the years being

TABLE 4

The Devon and Cornish spot-distributions for 1956 (compared with 1952 where available) ; males

Locality	Year	Spots						Totals
		0	1	2	3	4	5	
Okehampton, *Devon*	1952	...	...	14	6	2	...	22
,, ,,	1956	1	8	55	18	1	...	83
Lydford, *Devon*	1956	4	8	49	15	5	2	83
Lewannick, *Cornwall*	1952	2	2	25	4	2	...	35
,, ,,	1956	2	8	58	27	8	1	104

measured by $\chi^2_{(2)} = 7 \cdot 004$ at Okehampton, and by $\chi^2_{(2)} = 6 \cdot 228$ at Lydford, both giving P between $0 \cdot 05$ and $0 \cdot 02$. This indicates a shift from the Old English to the New English types within the typical Southern English female stabilisation : an adjustment which by 1956 had occurred widely in the rest of Southern England eastwards. The females of the Okehampton and Lydford populations for that year are evidently homogeneous (and see p. 375) when compared with one another, as they are when compared jointly with the nine " New

English " spot-distributions found east of Devon in the same season *
($\chi^2_{(3)} = 1 \cdot 14$, with P from $0 \cdot 8$ to $0 \cdot 7$).

In these nine " New English " populations, the females are
extremely homogeneous with one another ($\chi^2_{(16)} = 11 \cdot 144$). On the
other hand, the males are heterogeneous ($\chi^2_{(16)} = 30 \cdot 56$) being, as
usual in that sex, more prone to be independently adapted to the minor
environmental distinctions of each locality. The male spot-distri-
butions at Okehampton and Lydford (table 4) are, however, evidently
homogeneous in 1956.

We next proceeded to reinvestigate the nearest district previously
studied within the East Cornish stabilisation : that is to say, Lewannick.
Here we found that we could no longer obtain samples in the two
neighbouring localities where we collected in 1952. One was a large
sloping meadow which had now been ploughed. The other was a
narrow valley (SX292797) in which the grass had become much
invaded by bracken and brambles from the steep sides, so destroying
the greater part of the insect's habitat.

We accordingly searched the Lewannick neighbourhood for another
area where the butterfly was common. This we found just over three-
quarters of a mile eastwards, in the valley of the Inny near Drinnick
where the river is crossed by Trekelland Bridge (SX301797). The
sample obtained at this place showed a spot-distribution entirely
distinct in character from that of the Okehampton and Lydford
specimens, being of the East Cornish type (table 3) ; that is, bimodal
in the female. In that sex it was closely homogeneous with the con-
dition as established in the same district four years before ($\chi^2_{(3)} = 1 \cdot 092$,
with $P = 0 \cdot 8$ to $0 \cdot 7$), but it was only doubtfully so in the males
($\chi^2_{(1)} = 3 \cdot 007$, with $P = 0 \cdot 1$ to $0 \cdot 05$).

Owing, as it proves, to the small size of the sample which it was
possible to collect, it was in neither sex fully heterogeneous with the
estimate for the combined Okehampton and Lydford populations,
though it approached this in the females (for which the difference is
measured by $\chi^2_{(3)} = 6 \cdot 867$, with $P = 0 \cdot 1$ to $0 \cdot 05$; while for the males,
$\chi^2_{(3)} = 3 \cdot 575$, with P nearly $0 \cdot 3$). It will be shown, however, that the
" Lewannick " sample can be added to that from another East Cornish
population with which it is homogeneous. The difference between the
two combined, compared with the spot-distributions found in Devon,
is heavily significant in the females though not in the males (p.
376).

We therefore set out to analyse the transition between the two
types. This we did by sampling the *M. jurtina* population in the twelve
miles which separate these localities. We decided first to subdivide
the distance, which there includes the county boundary, into three
blocks, working from north-east to south-west. We accordingly

* Shapwick (Somerset), Middleton West (Hampshire), Worthy Down (Hampshire),
Shoreham (Sussex), Canterbury (Kent), Cothill (Berkshire), Rugby (Warwickshire), Ips-
wich (Suffolk), Holt (Norfolk).

advanced approximately four miles from Lydford finding, with some difficulty, a suitable collecting ground in a valley at Chillaton (SX435818). Here, to our surprise, the population proved completely Southern English in both sexes (tables 5 and 6).

TABLE 5

Spot-distributions in the localities sampled between the known Southern English (Lydford) and East Cornish (Lewannick) stabilisations in 1956 ; females

Locality	Spots						Total
	0	1	2	3	4	5	
Chillaton	38	18	13	6	3	...	78
Tamar West	30	19	9	5	1	1	65
East Larrick	20	11	6	1	...	...	38
West Larrick . . .	16	6	13	5	1	...	41

We next proceeded a further four and a half miles in the direction of the Lewannick area and discovered a locality near Hexworthy, in the Tamar valley on the west side of the river (SX366811), where the butterfly was in some numbers. It was, however, not easily caught,

TABLE 6

Spot-distributions in the localities sampled between the known Southern English (Lydford) and East Cornish (Lewannick) stabilisations in 1956 ; males

Locality	Spots						Total
	0	1	2	3	4	5	
Chillaton	...	9	63	17	9	...	98
Tamar West	3	7	59	20	2	...	91
East Larrick	...	6	51	22	3	...	82
West Larrick . . .	1	6	35	10	6	1	59

as the insects ranged widely at a rather low density over extensive fields. The resulting sample (tables 5 and 6) proved completely Southern English in spotting, without any indication that we were now within four miles of the " Lewannick " locality at the Inny Bridge which, as we knew, falls within the East Cornish stabilisation.

The intervening country, though irregular, on the whole rises from the valley of the Tamar until within a quarter of a mile of the Inny it drops steeply down to that river. We decided to advance approximately half-way across this area to Larrick, where we found a suitable collecting ground in the valley of a stream which runs eastward from the heights above the Inny valley. This stream is (at

SX329806) crossed by the lane from Launceston to Trebullett. The position is approximately two and a quarter miles from the population (proved Southern English) on the west side of the Tamar valley, and one and three-quarter miles from that, proved East Cornish, on the banks of the Inny. From here we moved westwards collecting on the southern side of the stream, keeping an account of our results on the way.

By the time we had worked through two fields before crossing a lane at Larrick farm and three subsequently, we had accumulated 82 males and 38 females. We accordingly paused on the east side of the hedge between the third and fourth fields from the farm (SX322803)
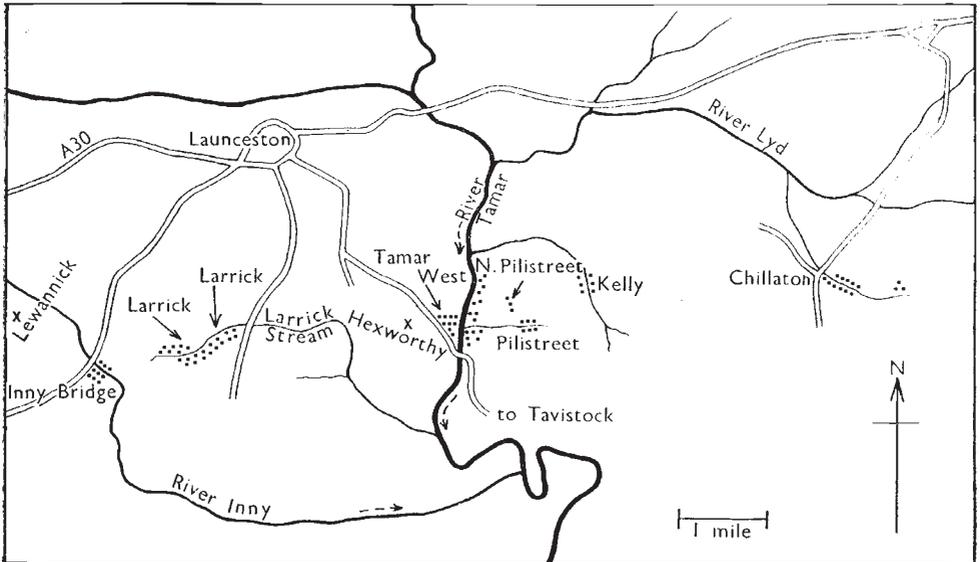

Fig. 3.—Map of the region in which we studied the transition from the Devon to the Cornish types of spotting in *Maniola jurtina*. The localities where the samples were obtained are indicated by dots. (The river Tamar is here the county boundary.)

and scored our sample (tables 5 and 6). Since we were making our way up the course of the stream, which ran beside us on our right, we describe this area as " East Larrick " (SX322 to 328 and 803 to 807). The result was still completely Southern English, though we were now no more than a mile and a quarter from the East Cornish population by the Inny Bridge (Lewannick). Indeed the spot-distributions found in the whole series of localities from Okehampton to this point (Okehampton, Lydford, Chillaton, Tamar West and East Larrick) are extraordinarily homogeneous. Their uniformity is measured by $\chi^2_{(8)} = 2 \cdot 741$ giving $P = 0 \cdot 95$ to $0 \cdot 9$ for the females, and by $\chi^2_{(8)} = 3 \cdot 662$ giving $P = 0 \cdot 9$ to $0 \cdot 8$ for the males.

We now climbed through the hedge and proceeded across the fourth field westwards from Larrick farm. It is of large size and the greater part is flat, but it slopes steeply down to the stream on its

northern side. As we advanced, making a rough assessment of our
captures on the way, we became aware that a change in spot-distri-
bution had at last occurred. We proceeded to collect in the next field
westwards and on some rough ground, interspersed with gorse and
bramble, separated from it by a narrow marshy copse. This marsh
continued the line of the stream which had, in fact, turned northwards
just previously.

These two fields, and the piece of rough ground beyond them, we
describe as the " West Larrick " locality (SX318322 and SX801803).
Having accumulated 59 males and 41 females there (tables 5 and 6),
we sat down to score them. The result was spectacular, confirming
the counts made while collecting. The females were completely
East Cornish in type, bimodal and highly homogeneous with the
Lewannick sample by the river Inny ($\chi^2_{(8)} = 0.512$, with $P = 0.95$-
0.90). They are heterogeneous when compared with those from East
Larrick in the fields immediately to the east ($\chi^2_{(2)} = 7.350$, with
$P = 0.05$-0.02).

When the females of the East Cornish stabilisation from West
Larrick and the Lewannick area (at the Inny Bridge) are combined,
which their extreme homogeneity fully allows, they may be com-
pared with the Southern English series from Okehampton to East
Larrick, itself already shown remarkably uniform. The result further
demonstrates the reality of the difference between these two types of
spot-distribution, for the heterogeneity between them is measured by
$\chi^2_{(3)} = 14.539$, giving $P = 0.01$-0.001.

The males, on the other hand, are moderately homogeneous with
the Southern English type at East Larrick ($\chi^2_{(3)} = 5.550$, with
$P = 0.2$-0.1). They are fully so with those of the Lewannick (Inny
Bridge) area ($\chi^2_{(3)} = 2.008$, with $P = 0.7$-0.5). The males from
West Larrick and Lewannick combined do not differ significantly
from the Southern English series from Okehampton to East Larrick
($\chi^2_{(3)} = 5.206$, with $P = 0.2$-0.1). As already explained, they do not
therefore provide a clear criterion of the distinction between the East
Cornish and main Southern English stabilisations.

When the female samples along the transect are compared, it is
found that the difference between the Southern English and the East
Cornish spot-distributions is greatest at the boundary between them.
This is most conveniently shown when the average spot-numbers are
considered. These are, of course, greater in the Cornish stabilisation,
with its subsidiary mode at 2, than in the Southern English, with its
single mode at 0. The values may be plotted against the distance
along the transect from a given datum point, in this case Lewannick
(see fig. 4). It will then be seen that the spot-average for West Larrick
is even higher than that for Lewannick, while that for East Larrick
is even lower than that for Tamar West. This is the precise opposite
of the situation found in a cline. No comparable effect can be detected
when the male spot-values are plotted in a similar manner.

The evidence consequently indicates that the Southern English and East Cornish spot-distributions change abruptly from one to the other. This they do within a few yards ; a transition which, in 1956, occurred at the ordinary field-hedge between the West and East Larrick collecting areas (SX322803). Yet this presents no barrier to the insects, which are constantly seen crossing it.
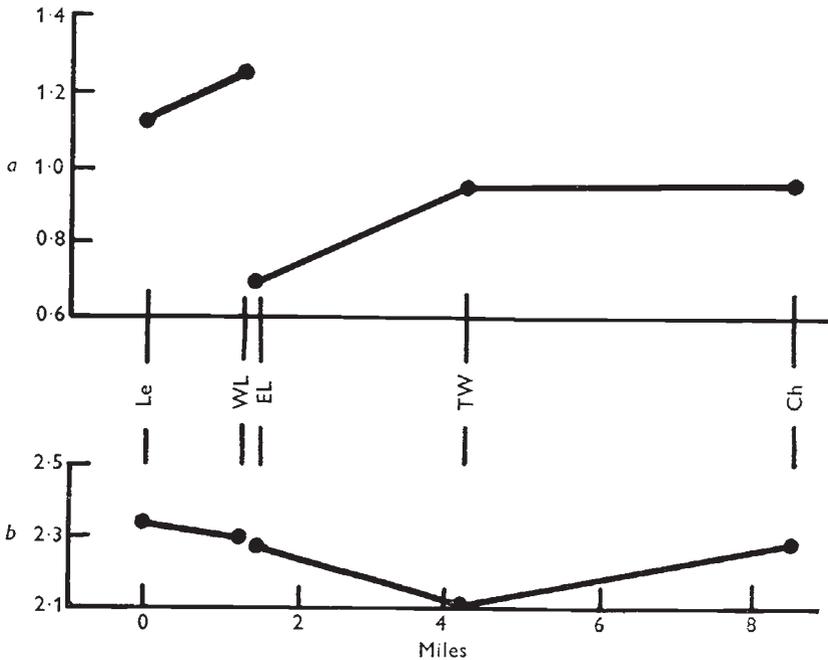
FIG. 4.—*Maniola jurtina* : the boundary between the East Cornish and Southern English stabilisations—1956. The average spot-numbers of (*a*) the females and (*b*) the males are plotted against the distance along the transect. For explanation see text page 376. (Le, Lewannick ; WL, West Larrick ; EL, East Larrick ; TW, Tamar West ; Ch, Chillaton.)

(iii) *Results obtained in* 1957

It was important to determine whether the abrupt discontinuity in spotting between the Southern English and East Cornish stabilisations, discovered in 1956, persisted the following year. We therefore again studied the spot-distributions of *Maniola jurtina* in the critical area of the Devon-Cornwall border in 1957. The work was more difficult than in the previous season because the butterfly was on the whole considerably rarer, due, no doubt, to the abnormal weather conditions of the spring and early summer. An unprecedented period of drought had continued up to early July and was followed by much rain for the rest of that month.

W. H. Dowdeswell, who collaborated in initiating these studies, and has great experience of them, accompanied us this year. We were joined also by E. R. Creed.

Our first objective was to collect in the Lewannick area at Inny Bridge, where we captured 126 males and 155 females (see tables 7 and 8). The two sexes were respectively homogeneous when compared with the samples obtained the previous year, the females being

TABLE 7

Spot-distributions in the localities sampled in the $8\frac{1}{4}$ miles from Chillaton (Devon) to Lewannick (Cornwall) in 1957 ; females. The localities are arranged from east to west

Locality	Spots						Total
	0	1	2	3	4	5	
Chillaton	27	19	10	5	...	...	61
Kelly	50	23	15	10	2	...	100
Pilistreet	51	20	8	6	...	...	85
N. Pilistreet . . .	26	11	8	4	1	...	50
Tamar West	84	32	41	12	...	...	169
East Larrick . . .	27	3	9	5	1	...	45
West Larrick . . .	1	2	...	...	1	...	4
Lewannick	80	23	43	8	1	...	155

TABLE 8

Spot-distributions in the localities sampled in the $8\frac{1}{4}$ miles from Chillaton (Devon) to Lewannick (Cornwall) in 1957 ; males. The localities are arranged from east to west

Locality	Spots						Total
	0	1	2	3	4	5	
Chillaton	...	8	42	15	4	1	70
Kelly	1	5	22	11	2	1	42
Pilistreet	...	...	25	12	2	...	39
N. Pilistreet . . .	...	3	25	9	3	...	40
Tamar West	2	4	35	9	4	2	56
East Larrick . . .	1	2	17	7	4	...	31
West Larrick . . .	...	1	3	...	...	...	4
Lewannick	2	7	79	29	9	...	126

bimodal (in that sex the comparison is measured by $\chi_{(3)}^{2} = 3 \cdot 912$, with $P = 0 \cdot 3$ to $0 \cdot 2$; while for the males $\chi_{(3)}^{2} = 1 \cdot 250$, with $P = 0 \cdot 8$ to $0 \cdot 7$). It was evident, therefore, that in 1957 the East Cornish type of spotting persisted unaltered in the Lewannick district.

We also collected on the west side of the river Tamar, near Hexworthy, in the locality studied in 1956 (p. 374). The butterflies were difficult to obtain, being widespread at a low density, so that it was necessary to spend two days there. However, we were at length

fortunate in discovering two fields in which considerable numbers were to be found in long grass. In all, we amassed 169 females and 56 males (see tables 7 and 8). Here we had been within the normal Southern English stabilisation the previous year, so we were surprised to find the females were now bimodal and completely of the East Cornish type.

Between the two localities so far studied (Inny Bridge and the west side of the Tamar near Hexworthy) lay the critical Larrick area which previously included the abrupt transition in spotting. Here *M. jurtina* was much rarer owing to the parched condition of the fields. The West Larrick locality was practically denuded of butterflies and a long search resulted only in 4 females and 4 males (see tables 7 and 8). The East Larrick region, being moister, was less unfavourable and there we amassed 45 females and 31 males (see tables 7 and 8) : a considerable number of these were caught in an orchard separated from the first field west of Larrick farm only by a stream narrow enough to jump over and a straggling hedge. It will be remembered that here in the previous year the females were of the normal Southern English type, being unimodal at o spots. They were now bimodal, the samples for 1956 and 1957 being heterogeneous ($\chi^2_{(2)}$ = 7·988, with P< ·02). This result accords with the similar situation two and a half miles farther east on the Cornish bank of the Tamar, suggesting that we had to deal with a change affecting a tract of country rather than independent adjustments to individual localities.

The spot-distributions in these three places, Lewannick, East Larrick and the west side of the Tamar, proved to be homogeneous (for the females, $\chi^2_{(6)}$ = 7·925, with P = 0·3 to 0·2 ; for the males, $\chi^2_{(6)}$ = 3·036, with P approximately 0·8). The 4 females and 4 males captured at West Larrick in 1957 are omitted from this calculation. Clearly it would not be right to include with East Larrick a sample too small to be judged independently, one from a population which had in fact been heterogeneous with it the previous year.

Thus the Cornish form of spotting evidently now affected the *jurtina* population as far east as the Tamar. It was necessary, therefore, at this stage to locate an unchanged English stabilisation as a preliminary to discovering whether or not the transition between the two types remained abrupt. Consequently we advanced four and a half miles to the next locality east of the Tamar where we had obtained information the previous year : that is to say, Chillaton. Here the Southern English stabilisation still persisted in 1957 (see table 7), the females being unimodal at o spots.

It was now clear that in the transect which we were studying, the change from the East Cornish to the Southern English spotting occurred somewhere between Chillaton and the Tamar ; presupposing, that is to say, that the distinctive types were to be found uniformly up to some transition area, broad or narrow, rather than in an independent scatter of localities. Consequently we looked for a suitable collecting

ground in this stretch of country. We found one in a valley at Kelly (SX388813) approximately two and three-quarter miles west of Chillaton. Here the *jurtina* population was still of the Southern English type, unimodal at 0 spots (see table 7), though we were now only one and a quarter miles east of the Tamar near Hexworthy.

At that point the river flows close to the eastern side of its flood-plain. A single row of fields about 150 yards wide separates it from a steep wooded bank, about 150 feet high, above which are open fields. We collected from the edge of these woods, at the top of the declivity, back for a few hundred yards, choosing the north side of a small valley near Pilistreet (SX375807). The sample obtained there was again completely Southern English, the females being unimodal at 0 spots. So too, was another (which we describe as North Pilistreet), running

TABLE 9

Spot-distributions of an intermediate type in the flood-plain, about 160 yards wide, east of the Tamar between the river and its escarpment

| | Spots | | | | | Total |
	0	1	2	3	4	
Females . .	67	36	34	5	...	142
Males . .	...	2	23	11	5	41

northwards for about 300 yards along the upper edge of the woods and separated from the last locality by about 150 yards (see table 7).

We had, therefore, explored a transect running from the edge of the Tamar Valley eastwards to Chillaton, approximately four miles away. The four populations included in it proved to be homogeneous in both sexes (for the females $\chi^2_{(9)} = 6 \cdot 239$, with $P > 0 \cdot 7$; for the males, $\chi^2_{(3)} = 0 \cdot 935$, with $P > 0 \cdot 8$).

We had now established that the Cornish and Southern English populations extended respectively west and east from the Tamar, each being homogeneous. The distinction between the bimodal Cornish and the unimodal English type of female is heavily significant, with $\chi^2_{(3)} = 18 \cdot 086$, giving $P < 0 \cdot 001$. The males as before, do not discriminate between the two stabilisations $(\chi^2_{(3)} = 1 \cdot 182$, with P between $0 \cdot 7$ and $0 \cdot 5)$.

In addition to the river itself (about 15 yards broad) and the precipitous woods from which the butterfly is absent, the English population at Pilistreet and the Cornish on the west bank of the Tamar are separated only by the eastern flood-plain, here no more than 150 yards wide, in which the butterfly is established and in which with difficulty we amassed a considerable sample (see table 9). This proved to be significantly intermediate in type, with nearly equal values at one and two spots in the female. In that sex, the differences involved

are measured as follows : when compared with the Cornish form, from Lewannick to the west bank of the Tamar, $\chi^2_{(3)} = 8\cdot022$ (with $P = 0\cdot05$-$0\cdot02$), while compared with the Southern English form, from Chillaton to North Pilistreet, $\chi^2_{(3)} = 10\cdot663$ (with $P < 0\cdot02$).

We attempted two further collections in what might be intermediate areas. One of these (A, see table 10) consisted of two contiguous fields, carved out of the hanging woods which here isolate the eastern flood-plain from the Pilistreet locality. At the bottom, one of them is separated only by a line of trees from the plain itself. We could only obtain a few butterflies here. These were probably of the intermediate type, but the numbers are too small to be decisive. The other sample (B, see table 10) was caught in a steeply sloping field running south

TABLE 10

(*See text*)

Localities	Spots					Total
	0	1	2	3	4	
A (males) .	...	...	5	4	...	9
(females) .	3	5	4	1	...	13
B (males) .	...	3	14	11	1	29
(females) .	14	8	5	2	...	29

along the top of the woods from the Pilistreet area. Its spot-distribution appears to be typical Southern English, as is to be expected here, but the numbers seem hardly large enough to warrant inclusion in the general calculations.

When a comparison is made of the average spot-numbers for the samples along the transect, in a similar manner to that for the 1956 results (p. 376), an effect representing the reverse of a cline is again obtained in the females (see fig. 5). However, this time the divergence from the normal is confined to the English side of the boundary (the Pilistreet, though not the North Pilistreet sample). It should be pointed out that, owing to the higher mode at 0 spots, the average spot-numbers of the East Cornish samples are rather lower than in 1956.

In the males the condition in 1957 differs not only from that in the females but also from that in the males the previous year. In 1956 their spot-averages did not vary at the boundary. In 1957 (see fig. 5) the male samples from the English population at Pilistreet and from the intermediate one at Tamar East, have higher spot-averages than the other English or East Cornish samples, whereas the females from Pilistreet have a considerably lower spot-average than is obtained either to the east or west.

Powerful selection-pressures are no doubt operating universally

on *Maniola jurtina*. The reverse cline effect observed at the junction between the East Cornish and Southern English stabilisations in both 1956 and 1957 suggests that here they are of quite exceptional force.
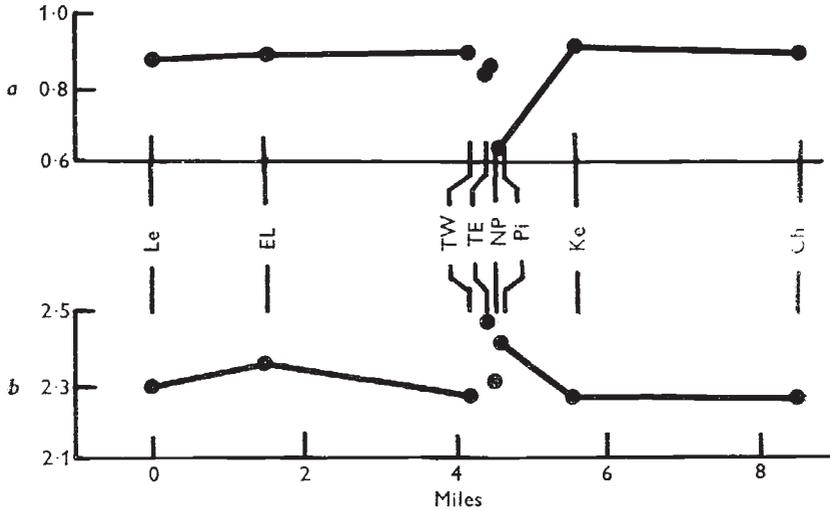

FIG. 5.—*Maniola jurtina* : the boundary between the East Cornish and Southern English stabilisations—1957. The average spot-numbers of (*a*) the females and (*b*) the males are plotted against the distance along the transect. For explanation see text pages 376 and 381. (Le, Lewannick ; EL, East Larrick ; TW, Tamar West ; TE, Tamar East ; NP, North Pilistreet ; Pi, Pilistreet ; Ke, Kelly ; Ch, Chillaton.)

3. DISCUSSION

The most striking of the facts communicated above is the sudden change from the South English (N.E.) to the East Cornish (E.C.) stabilisation (pp. 371-82). Before we undertook the task of transecting the boundary between these two stabilisation areas we thought we might find, in the following order of likelihoods, (i) a steep cline, or (ii) isolation, *i.e.* a region in which *M. jurtina* was rare or absent, or (iii) a confused pattern, in which populations with various or intermediate spot-frequencies could be found. It was, therefore, very surprising to find firstly, that the change occurred abruptly at a point where there was no barrier to *M. jurtina* and where the population was as dense as it was anywhere else on the transect, and secondly, that in the immediate neighbourhood of the boundary the female spot-distributions on each side actually diverged from one another, producing the effect which we describe as the precise opposite of a cline (p. 376).

Our findings in 1956 could be interpreted in two ways : (*a*) that the two populations were genetically isolated, or (*b*) that different norms of selection, acting on a genetically continuous population, were in force on either side of the boundary and that the geographic transition from one norm to the other was sharp. The discovery in

1957 that the clear-cut boundary between the two stabilisation areas had shifted some three miles eastward forced us to reject explanation (*a*) above and to accept (*b*). Clearly, in view of the life-history of *M. jurtina* no population could spread and replace another as rapidly and extensively as would be indicated by a shift of three miles per annum along this transect. Thus we visualise the South English-east Cornish boundary as one at which there is a change-over, not between genetically isolated populations, but between one set of selectional forces and another.

Turning to the data obtained in the former South English stabilisation area, the same kind of explanation offers itself irresistibly. We cannot easily imagine any process of population-replacement causing the change from O.E. to N.E. or P.C. spot-distributions, especially when two of these occur consecutively during the emergence at one locality. It is clear that populations of *M. jurtina* are subject to powerful, yet buffered, selection-pressures which are occasionally liable to change.

We have no hesitation in postulating strong selection-pressures. Let us consider two closely studied polymorphisms : Allison (1954) finds that the fitness of sickle-cell heterozygotes in Man is 1·26 times that of the normal homozygote in regions of East Africa where malaria is hyperendemic ; Kettlewell (1958), discussing the spread of melanism in *Biston betularia* (L.) since the Industrial Revolution, postulates selective advantages in favour of the *carbonaria* gene rising to around 30 per cent. The spot-phenotypes of *M. jurtina* seem likely to be controlled by a polygenic system, but strong selection can, of course, still operate on characters governed simultaneously by several genes.

It is tempting to try to identify the selectional forces involved, in the case of *M. jurtina*, although these are immaterial to our thesis if it is admitted that spot-phenotypes are entirely or mainly genetically determined. Conclusive proof can only be obtained from individual breeding experiments, which, despite the great technical difficulties of controlled mating in the *Satyridæ*, we hope to perform. Existing data on a population basis, however, indicate that tendencies towards high or low spotting can be inherited from one year to another and we shall present a separate analysis dealing with this point.

In the Isles of Scilly we have noticed some degree of correlation between high spot-values and relative luxuriance of the habitat (McWhirter, 1957) and it was an obvious approach to an explanation of the sudden outbreak of high-spotting all over Southern England to examine whether this could be explained by the decimation of the rabbit population after the rapid spread of the virus disease, myxomatosis ; in many areas this produced a lush growth of grasses, including those which are food-plants of *M. jurtina*. Such an hypothesis, however, can hardly be maintained. It is known that rabbits have been absent from Oxford, Medley Manor, since 1947, when they were destroyed by high floods ; they had had no opportunity to recover before myxomatosis appeared. Yet the *M. jurtina* population in the vicinity

has conformed to the general pattern (1956, P.C. ; 1957, P.C. then O.E.).

There are three types of discontinuity of spot-distributions discussed in this paper ; local (especially in the region of the extraordinarily sharp boundary between the South English and East Cornish stabilisation areas), inter-seasonal and intra-seasonal. All three of these show a kind of " quantum " effect which is reflected in triangular diagrams such as figs. 1 and 2 above and in fig. 2 in McWhirter (1957), where data from the Isles of Scilly are similarly treated. In all these diagrams " clumping " of the entries is strongly marked. The true explanation of these effects will, we hope, emerge from further investigations.

4. SUMMARY

1. Between 1953 and 1955 the well-established South English stabilisation area, in which all populations of *M. jurtina* had female spot-distributions with large modes at o spots, broke up.

2. Two new types of distribution have appeared in this area, involving higher levels of spotting in both males and females, and these are defined.

3. The wave of high spotting reached a peak in 1956 and receded in 1957.

4. The inception of a new stabilisation area confined to the southwestern part (Devon, Somerset and Dorset) of the former South English stabilisation area is described.

5. Not only local and inter-seasonal, but also intra-seasonal shifts in spot-distribution are now known in several places.

6. In some cases high spotting seems to have spread through a population after being at first confined to the early part of the emergence.

7. In 1952 it had been shown that while female spotting is unimodal at o spots in all areas sampled from the North Sea to west Devon, it is bimodal (with a greater mode at o and a lesser at 2 spots) in east Cornwall. These two types were stabilised in spite of great environmental differences within the regions they inhabit and persisted to within twelve miles of one another.

8. They still remained distinct in west Devon and east Cornwall in 1956.

9. The country separating them was studied in that year. It was then found that one type was replaced by the other in a few yards, at a single field-hedge which was not a barrier to the insect's movement.

10. The two populations proved to be subject to a phenomenon which represents the reverse of a cline. That is to say, their differences in spotting became accentuated as the boundary between them was closely approached.

11. This general situation persisted in 1957 when the boundary

separating the West Devon and East Cornish forms had, in the transect we were studying, moved three miles eastwards, to the river Tamar. It was, however, slightly less sharp since an intermediate population inhabited the eastern flood-plain, here only about 150 yards wide.

12. An effect representing the reverse of a cline could again be detected in 1957, for the characteristics of the West Devon, though this season not of the East Cornish, form were accentuated at the point where the two approached most closely.

13. It is argued that the most likely explanation of the sharp boundary at the Cornish border and of the sudden large changes in the South English populations is that strong selective forces operate on characters connected with spotting ; these forces differ locally and, sometimes, when a stabilisation area passes into a fluid state, they appear to differ temporally.

14. We have considered, but regard as inconclusive, the evidence that the spread of the virus disease, myxomatosis, which has decimated the rabbit population and encouraged lush growth of grasses in many parts of Southern England, might be responsible for the wave of high-spotting which reached a peak in 1956.

15. Data from areas round the periphery of the former South English stabilisation area (Lundy Island, Isle of Man, Sutherland and Normandy) are briefly considered.

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2 B

APPENDIX 1

Spot-distributions of Maniola jurtina, *1956*

(The serial numbers in the left-hand column refer to the corresponding entries in fig. 1.)

Locality		Spots						Total	Spot-av.
		0	1	2	3	4	5		
1. Canterbury, *Kent* .	♂	4	5	45	21	...	...	75	2·11
	♀	17	10	6	2	...	...	35	0·80
2. Chillaton, *Devon* .	♂	...	9	63	17	9	...	98	2·27
	♀	38	18	13	6	3	...	78	0·95
3. Chelmsford, *Essex* .	♂	1	3	27	14	2	...	47	2·28
	♀	7	8	5	3	...	...	23	1·17
4. Cothill, *Berkshire* .	♂	...	5	38	21	2	...	66	2·30
	♀	14	10	7	2	1	...	34	1·00
5. East Larrick, *Cornwall*	♂	...	6	51	22	3	...	82	2·27
	♀	20	11	6	1	...	...	38	0·68
6. Holt, *Norfolk* .	♂	3	10	105	41	9	1	169	2·27
	♀	27	19	13	3	1	...	63	0·92
7. Ipswich, *Suffolk* .	♂	1	2	65	38	8	...	114	2·44
	♀	42	32	23	7	1	...	105	0·98
8. Lewannick, *Cornwall*	♂	2	8	58	27	8	1	104	2·33
	♀	44	18	30	10	2	...	104	1·12
9. Lydford, *Devon* .	♂	4	8	49	15	5	2	83	2·18
	♀	50	27	20	11	...	...	108	0·93
10. Middleton East, *Hampshire* .	♂	2	5	32	8	...	...	47	1·98
	♀	93	43	12	...	...	...	148	0·45
11. Middleton West, *Hampshire*	♂	4	9	79	18	7	...	117	2·13
	♀	50	30	15	7	...	...	102	0·79
12. Newbury, *Berkshire* .	♂	1	1	12	7	2	...	23	2·35
	♀	5	2	4	...	...	...	11	0·91
13. Newton Abbot, *Devon*	♂	4	14	59	23	6	...	106	2·12
	♀	60	23	15	2	1	...	101	0·62
14. Noss Mayo, *Devon* .	♂	2	8	87	37	8	3	145	2·34
	♀	31	21	12	1	1	...	66	0·79

APPENDIX 1—*continued*

Spot-distributions of Maniola jurtina, *1956*

Locality		Spots						Total	Spot-av.
		0	1	2	3	4	5		
15. Okehampton, *Devon*	♂	1	8	55	18	1	...	83	2·12
	♀	45	29	20	5	...	...	99	0·85
16. Oxford, Medley Manor	♂	1	30	120	69	30	2	252	2·41
	♀	44	22	29	8	2	...	105	1·07
17. Oxford, Parks .	♂	1	7	31	13	8	...	60	2·33
	♀	5	5	3	...	...	...	13	0·85
18. Plymouth, Roborough, *Devon*	♂	2	2	10	7	...	...	21	2·05
	♀	20	1	6	5	...	...	32	0·88
19. Rugby, *Warwickshire*	♂	3	19	70	30	2	2	126	2·12
	♀	27	23	14	8	2	...	74	1·12
20. Shapwick, *Somerset*	♂	1	2	35	12	3	...	53	2·26
	♀	18	11	9	1	...	...	39	0·82
21. Sherborne, *Dorset* .	♂	5	11	82	29	5	...	132	2·14
	♀	28	10	7	3	...	...	48	0·69
22. Shoreham, *Sussex* .	♂	...	8	60	17	1	...	86	2·13
	♀	21	14	6	1	1	...	43	0·77
23. Taunton, *Somerset* .	♂	...	2	30	19	3	...	54	2·43
	♀	12	3	5	1	...	...	21	0·76
24. Tamar West, *Cornwall*	♂	3	7	59	20	2	...	91	2·12
	♀	30	19	9	5	1	1	65	0·94
25. Tiverton, *Devon* .	♂	...	7	57	38	6	...	108	2·40
	♀	47	18	23	8	1	...	97	0·95
26. West Larrick, *Cornwall*	♂	1	6	35	10	6	1	59	2·29
	♀	16	6	13	5	1	...	41	1·24
27. Woolbury Ring, *Hampshire*	♂	...	3	42	13	3	...	61	2·26
	♀	38	18	8	3	1	...	68	0·69
28. Worthy Down, *Hampshire*	♂	2	7	73	35	2	1	120	2·26
	♀	60	40	17	3	1	...	121	0·72

APPENDIX 2

Spot-distributions of Maniola jurtina, *1957*

(The serial numbers in the left-hand column refer to the corresponding entries in fig. 2.)

Locality		Spots						Total	Spot-av.
		0	1	2	3	4	5		
*29. Birdlip, *Gloucestershire* (to 21/vii)	♂	...	4	25	8	5	...	42	2·33
	♀	6	6	3	...	...	...	15	0·80
30. Birdlip, *Gloucestershire* (28/vii)	♂	...	...	7	1	1	...	9	2·33
	♀	29	9	6	1	...	...	45	0·53
31. Canterbury, *Kent* .	♂	...	1	23	3	...	...	27	2·07
	♀	12	4	4	...	...	...	20	0·60
32. Chillaton, *Devon* .	♂	...	8	42	15	4	1	70	2·26
	♀	27	19	10	5	...	...	61	0·89
33. East Larrick, *Cornwall*	♂	1	2	17	7	4	...	31	2·35
	♀	27	3	9	5	1	...	45	0·89
34. Heswall, *Cheshire* .	♂	3	12	47	10	4	...	76	2·00
	♀	28	10	7	2	...	...	47	0·64
35. Hoylake, *Cheshire* .	♂	2	5	22	4	1	...	34	1·91
	♀	20	3	5	...	...	...	28	0·46
36. Holt, *Norfolk* .	♂	4	12	128	39	9	...	192	2·19
	♀	66	21	8	1	...	1	96	0·47
37. Intermediate " A ", *Devon*, (p. 381)	♂	...	...	5	4	...	...	9	2·44
	♀	3	5	4	1	...	...	13	1·23
38. Intermediate " B ", *Devon* (p. 381)	♂	...	3	14	11	1	...	29	2·34
	♀	14	8	5	2	...	...	29	0·83
*39. Ipswich, *Suffolk* (to 6/vii)	♂	1	19	135	44	9	2	210	2·22
	♀	11	8	4	3	...	...	26	0·96
40. Ipswich, *Suffolk* (from 20/vii)	♂	92	32	49	20	8	1	82	2·40
	♀	91	33	13	2	1	...	140	0·49
41. Kelly, *Devon* . .	♂	1	5	22	11	2	1	42	2·26
	♀	50	23	15	10	2	...	100	0·91
42. Lewannick, *Cornwall*	♂	2	7	79	29	9	...	126	2·29
	♀	80	23	43	8	1	...	155	0·88

APPENDIX 2—*continued*

Spot-distributions of Maniola jurtina, *1957*

Locality		Spots						Total	Spot-av.
		0	1	2	3	4	5		
43. Middleton East, *Hampshire*	♂	7	25	164	37	6	...	239	2·04
	♀	126	41	20	3	...	...	190	0·47
44. Middleton West, *Hampshire*	♂	2	7	71	16	8	...	104	2·20
	♀	48	16	5	...	...	...	69	0·38
45. Newbury, *Berkshire*.	♂	...	7	50	23	9	1	90	2·41
	♀	25	8	17	1	...	...	51	0·88
46. North Pilistreet, *Devon*	♂	...	3	25	9	3	...	40	2·30
	♀	26	11	8	4	1	...	50	0·86
47. Newton Abbot, *Devon*	♂	1	3	24	6	...	...	34	2·03
	♀	32	20	8	2	...	...	62	0·68
*48. Oxford, Medley Manor (to 5/vii)	♂	4	23	127	17	4	...	175	1·97
	♀	25	17	21	5	...	...	68	1·09
49. Oxford, Medley Manor (24/vii)	♂	...	6	14	6	...	1	27	2·11
	♀	16	9	2	1	...	...	28	0·57
*50. Oxford, Parks (7/vii)	♂	2	10	56	16	5	...	89	2·13
	♀	54	21	23	6	...	...	104	0·82
51. Oxford, Parks (23, 29/vii)	♂	...	6	25	8	1	...	40	2·10
	♀	53	19	11	1	...	1	85	0·58
52. Pilistreet, *Devon*	♂	...	...	25	12	2	...	39	2·41
	♀	51	20	8	6	...	...	85	0·64
53. Rugby, *Warwickshire*	♂	1	1	16	4	...	...	22	2·05
	♀	11	2	2	...	...	...	15	0·40
54. Sherborne, *Dorset* .	♂	...	6	57	12	2	...	77	2·13
	♀	21	11	7	1	...	...	40	0·70
55. Taunton, *Somerset* .	♂	2	7	75	20	2	...	106	2·12
	♀	15	11	9	3	...	...	38	1·00
56. Tamar East, *Devon*	♂	...	2	23	11	5	...	41	2·46
	♀	67	36	34	5	...	...	142	0·84
57. Tamar West, *Cornwall*	♂	2	4	35	9	4	2	56	2·27
	♀	84	32	41	12	...	...	169	0·89
58. Tiverton, *Devon* .	♂	1	3	37	10	3	1†	55	2·27
	♀	8	11	6	3	...	...	28	1·14
59. Worthy Down, *Hampshire*	♂	4	9	71	20	3	...	107	2·08
	♀	73	27	11	3	...	...	114	0·51

* Arbitrary divisions have been made in these sets of data to illustrate the difference between the early and later parts of the emergence. Copies of these data giving complete details of dates of capture have been deposited in the Radcliffe Library, Oxford.

† This specimen had six spots.

APPENDIX 3

Data indicating intra-seasonal homogeneity at two locations in 1957

Locality		Spots						Total	Spot-av.
		0	1	2	3	4	5		
Middleton East, *Hampshire* (18/vi)	♂	1	6	43	11	...	...	61	2·05
(30/vi)	♂	1	2	14	4	...	...	21	2·00
	♀	9	1	...	1	...	...	11	0·36
(6/vii)	♂	5	14	84	22	6	...	131	2·08
	♀	21	7	6	...	...	...	34	0·56
(27/vii)	♀	42	13	3	...	...	...	58	0·33
(1/ix)	♂	...	2	17	...	...	...	19	1·89
	♀	32	14	7	2	...	...	55	0·62
(2/ix)	♂	...	1	6	...	...	...	7	...
	♀	22	6	4	...	...	...	32	0·44

If the females are classed into those at 0 spots and those at one or more than one spots, and if the samples are grouped into early (30/vi and 6/vii), middle (27/vii) and late (1/ix and 2/ix) emergences, then $\chi^2_{(2)} = 1\cdot67$; $0\cdot5 > P > 0\cdot3$.

Locality		Spots						Total	Spot-av.
		0	1	2	3	4	5		
Middleton West, *Hampshire* (18/vi)	♂	1	5	33	6	5	...	50	2·18
	♀	1	1	...	...	...	...	2	...
(6/vii)	♂	...	1	30	9	2	...	42	2·29
	♀	12	5	2	...	...	...	19	0·47
(27/vii)	♂	1	1	8	1	1	...	12	2·00
	♀	15	6	2	...	...	...	23	0·43
(16/viii)	♀	20	4	1	...	...	...	25	0·24

Classifying the females as above in the case of Middleton East, $\chi^2_{(2)} = 2\cdot07$; $0\cdot5 > P > 0\cdot3$.

APPENDIX 4

Data indicating intra-seasonal shift from populations at Burham Down, Kent,
scored by J. D. F. Frazer

Locality		Spots						Total	Spot- av.
		0	1	2	3	4	5		
Locality " A ", 1955 (to 23/vii)	♂	...	3	58	6	3	...	70	2·13
	♀	18	4	11	2	...	...	35	0·91
(after 23/vii)	♂	5	15	110	5	...	1	136	1·88
	♀	208	36	19	2	...	...	265	0·30
Locality " A ", 1956 (to 22/vii)	♂	4	36	308	92	18	3	461	2·20
	♀	48	15	20	4	...	...	87	0·77
(26/vii-2/viii)	♂	...	6	69	13	3	1	92	2·17
	♀	21	5	2	...	...	...	28	0·32
(after 2/viii)	♂	4	7	82	1	1	...	95	1·87
	♀	105	29	14	3	1	...	152	0·46
Locality " A ", 1957 (to 30/vi)	♂	2	15	256	73	23	6	375	2·31
	♀	27	6	15	5	...	...	53	0·96
(7 and 10/vii)	♂	1	8	83	20	8	...	120	2·22
	♀	32	9	3	5	...	...	49	0·61

Arbitrary divisions have been made in these data to illustrate the differences between the various phases of the emergences. Each phase appears to be quite homogeneous and to be sharply distinguishable from other phases of the same emergence : all these data will be the subject of further, more detailed analysis. Both sexes appear to change simultaneously in 1955 ; in 1956 there is a short period during which the females have changed but not the males ; in 1957 there is no evidence of any change in the males up to July 10.

Copies of these data giving complete details of dates of capture and some further information concerning Locality " B " (two miles from Locality " A "), where no intra-seasonal shift could be detected in 1957, have been deposited in the Radcliffe Library, Oxford.