EVOLUTIONARY STUDIES ON *MANIOLA JURTINA* (*LEPIDOPTERA SATYRIDAE*)

THE SOUTHERN ENGLISH STABILISATION, 1961-68

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1. Introduction

In a previous paper (Creed *et al.*, 1962) covering studies of the Meadow Brown butterfly, *Maniola jurtina*, on the English Mainland during the years 1958-60, we were concerned not only with the populations of southern England but also with peripheral colonies in Wales, Scotland, Ireland and elsewhere. The present account is more restricted in scope and is based largely on the extensive data obtained from the Winchester and Ipswich areas during the last eight years. No mention will be made here of the situation occurring further west in Devon and Cornwall (" Boundary Phenomenon ") since this is the subject of a separate paper (Creed *et al.*, 1969).

The principal findings so far of the studies on *Maniola jurtina* have now been summarised (Ford 1965, chs. 4 and 5). The pattern of spotting on the hind-wings of the insect has been shown to provide a reliable and sensitive index of variation. Thus, across southern England from Devon eastwards, the spot-distribution is unimodal in both sexes; at 2 spots in the males and at 0 in the females. We have called this the *Southern English* pattern. Different spot-stabilisations are found in other parts of the animal's range, particularly in peripheral areas such as the Isles of Scilly (Creed *et al.*, 1964) and North-West Africa (Dowdeswell and McWhirter, 1967). Such sharply deviant stabilisations affecting the basic pattern of spot-distribution, can be regarded as " first-order " variations.

In a previous paper (Creed *et al.*, 1962) we have emphasised the occurrence of " second-order " variations in spotting—those which occur both within a single season (intra-seasonal) and between one year and another (inter-seasonal) but always within the framework of first-order distinctions. To illustrate their more extreme form, we have found populations in which the proportion of spotless females fluctuated between 60 per cent. or more of the total (Old English type) and considerably fewer than 60 per cent. (New English). However, second-order fluctuations are often of lesser magnitude and a convenient way of quantifying them is by means of the spot-average (scoring, as a convention, the left hind wing of each insect). This is obtained by multiplying the class values by their frequencies, summating and dividing by the total.

2. Winchester

In the Winchester area, populations of *M. jurtina* are large and this has facilitated regular sampling during the last eight years in June-July (" early " sample) and in August (" late " sample). The complete data are rather voluminous and in the interest of brevity, only a summary is included here (table 1). The full results can be obtained from the data depository of the British Museum (Natural History).

In table 1, the column for " Probability " provides information on the homogeneity of each set of samples. Evidently most of the results from successive years are highly heterogeneous so, on statistical grounds, there is no justification for combining them. In interpreting them, the two components

Table 1

Summary of samples of M. jurtina *from the Winchester area (1961-68)*

Date	Sex	Spots 0	1	2	3	4	5	Total	Probability	Spot-average	Range of variation
June-July	Male	16	70	808	260	75	5	1234	0·01>P>0·001	2·26	2·12-2·41
August	Male	6	27	413	85	14	2	547	0·3>P>0·2	2·15	2·01-2·25
June-July	Female	492	329	209	94	10	–	1134	0·05>P>0·02	0·94	0·74-1·21
August	Female	505	198	104	22	2	–	831	<0·001	0·58	0·42-0·97

must, as it were, be pulled apart. Thus, the first-order distinction (males unimodal at 2 spots and females unimodal at 0) has been extraordinarily consistent throughout, while the second-order differences (the various frequencies existing within the first-order range) have fluctuated considerably (figs. 1 and 2).

The general picture emerging from the Winchester area is one of extreme stability of spotting in so far as first-order variation is concerned. The males maintained consistently the characteristic high mode at 2 spots, while the females were unimodal at 0. However, the populations have been subject to considerable second-order variation. As might be expected, this was particularly noticeable as between one year and another, and accounts for the high degree of heterogeneity in the early males and late females (table 1). Of considerable interest too, is the marked intra-seasonal spot-variation, a feature of many *jurtina* populations to which we first drew attention in 1959 (Creed *et al.*). As will be seen from the Winchester data, this took the form of a small but consistent reduction in spot-average as the season advanced, the overall range of variation remaining about the same. In the females the reduced spotting was more marked, the seasonal decline averaging 38 per cent. during the last eight years. Thus, unspotted females comprised 43 per cent. of the early samples (New English) and 61 per cent. of the late ones (Old English). As in the males, the range of variation in spot-average remained more or less unaltered between early and late emergences.

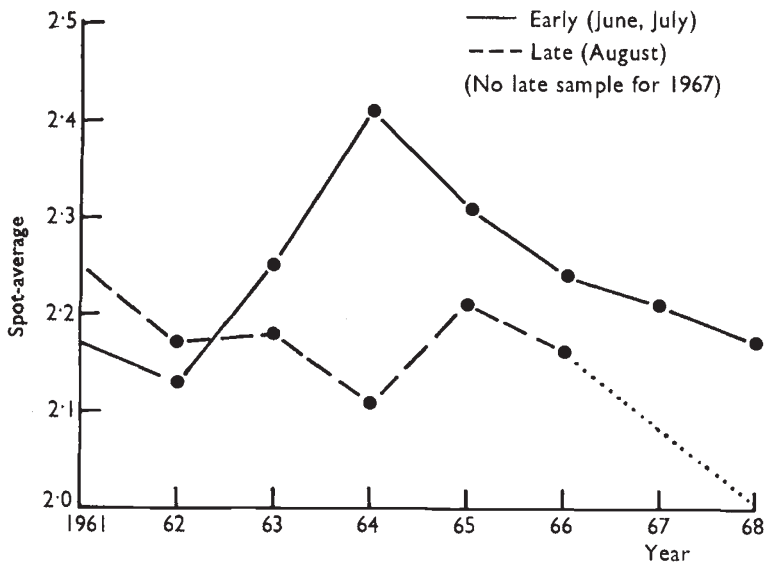

FIG. 1.—Intra-seasonal variation in *M. jurtina* males from the Winchester area (1961-68).

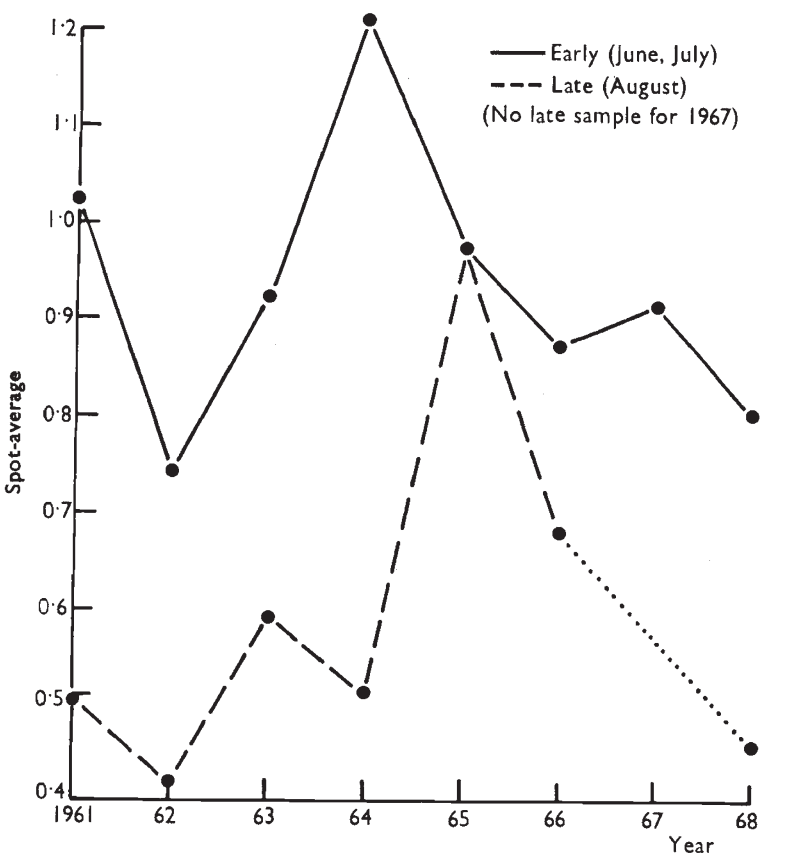

FIG. 2.—Intra-seasonal variation in *M. jurtina* females from the Winchester area (1961-68).

3. Ipswich

The *M. jurtina* populations of the Ipswich area are the only ones in eastern England for which we have extensive data (figs. 3 and 4) comparable with

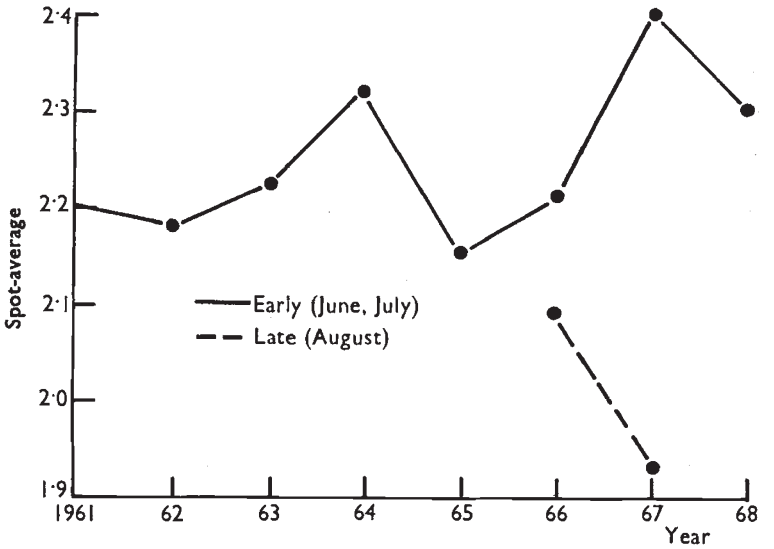

Fig. 3.—Intra-seasonal variation in *M. jurtina* males from the Ipswich area (1961-68).

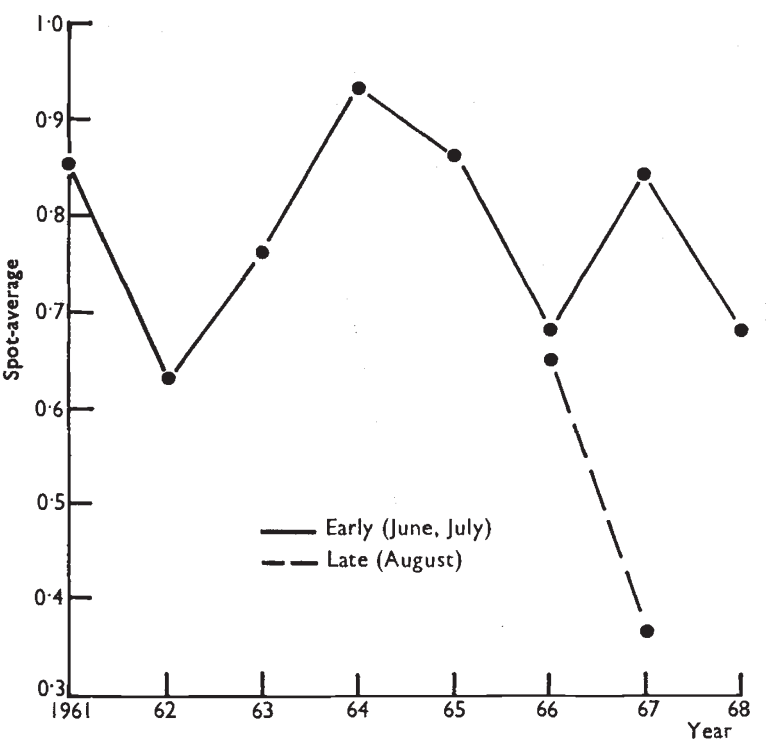

Fig. 4.—Intra-seasonal variation in *M. jurtina* females from the Ipswich area (1961-68).

those from Winchester. Thus, samples for the last eight years have been summarised in table 2, using the same procedure as already outlined for table 1.

While a formal comparison between Ipswich and Winchester is impossible owing to the heterogeneity of the respective sets of samples, it is nonetheless striking how consistently more homogeneous the Ipswich samples are than those from Winchester (tables 1 and 2). In the former, the only heterogeneity occurs among the late females, and it is particularly interesting that the very same group is vastly more variable at Winchester.

TABLE 2

Summary of samples of M. jurtina *from the Ipswich area (1961-68)*

		Spots									
Date	Sex	0	1	2	3	4	5	Total	Proba-bility	Spot-average	Range of variation
June-July	Male	24	119	1055	314	97	12	1621	0·1>P>0·05	2·23	2·12-2·40
August	Male	1	12	53	10	1	–	77	0·7>P>0·5	1·97	1·93-2·09
June-July	Female	434	220	140	49	3	–	846	0·3>P>0·2	0·78	0·68-0·93
August	Female	125	42	22	4	–	–	193	0·05>P>0·02	0·51	0·37-0·65

Throughout the eight years, the general pattern of spot-variation in the two populations was very similar in both sexes. The males maintained a consistently high mode at 2 spots, averaging 65 per cent. in the early samples (compared with 66 per cent. at Winchester) and 69 per cent. in the late ones (Winchester 76 per cent.). The relatively low totals for the late samples are due to the fact that these were only available for 1966 and 1967. As in the Winchester populations, the pattern of intra-seasonal spot-variation involved reduction in spotting as the season proceeded, that in the females being more pronounced than in the males. The range of variation remained more or less constant in both sexes.

4. OTHER SOUTHERN ENGLISH POPULATIONS

We have also obtained intermittent samples of *M. jurtina* from a small number of other localities which, together, span much of southern England—Tilshead (Wiltshire), Oxford, Elsfield (Oxfordshire), Holyport (Berkshire) and Hatfield Forest (Essex). Although the data are less extensive than those from Winchester and Ipswich, they nonetheless provide a useful check on the extent of the southern English spot-stabilisation. With the exception of the sample from Hatfield Forest which merits separate treatment, the remaining results are summarised in table 3.

The dates of the samples from Tilshead fall strictly outside the period under review. They have, however, been included here since we have not published them previously and they are relevant to the present discussion. The two samples from Tilshead and the three from Elsfield are small and homogeneous and each set can therefore be accumulated. A comparison of all the males shows the samples to be heterogeneous ($\chi^2_{(3)} = 14{\cdot}19$;

$0{\cdot}01 > P > 0{\cdot}001$) while that of the females, after combining the Oxford and Elsfield samples which are geographically close, gives $\chi^2_{(6)} = 7{\cdot}48$; $0{\cdot}3 > P > 0{\cdot}2$, indicating homogeneity in this sex.

TABLE 3

Summary of samples of M. jurtina *from four localities in Southern England (1959-67)*

Locality	Date	Sex	Spots 0	1	2	3	4	5	Total	Spot-average
Tilshead	July 1959-60	Male	—	4	50	21	5	1	81	2·37
Oxford	June 1961	Male	—	1	22	2	1	—	26	2·12
Elsfield	June-August 1961-63	Male	—	16	94	15	3	—	128	2·04
Holyport	July 1967	Male	—	3	30	5	—	—	38	2·05
Tilshead	July 1959-60	Female	37	17	13	8	—	—	75	0·89
Oxford	June 1961	Female	5	5	4	—	—	—	14	0·93
Elsfield	June-August 1961-63	Female	27	18	13	5	2	—	65	1·03
Holyport	July 1967	Female	35	32	28	15	2	—	112	1·26

Clearly, the stabilisation in males and females characteristic of Winchester and Ipswich, is a feature of these populations as well. All the samples (including most of those from Elsfield) were taken " early ", and this is reflected in the spot-averages of both sexes which tend to be on the high side, as we would expect.

In 1963, we received a remarkable sample of *M. jurtina* from a locality in Hatfield Forest near Bishop's Stortford, summarised in table 4.

TABLE 4

Sample of M. jurtina *from Hatfield Forest (1963)*

Date	Sex	Spots 0	1	2	3	4	5	Total	Spot-average
31 July	Male	—	1	48	11	3	—	63	2·25
31 July	Female	17	29	16	7	—	—	69	1·19

Bearing in mind that this was a relatively late sample, spotting in the males was quite typical and similar to that at Winchester. Spot-distribution in the females was, however, unique for this part of southern England, being unimodal at 1 spot. Unfortunately, we have not had an opportunity of obtaining further samples from this interesting locality, so we are unable to tell whether we were witnessing a sporadic fluctuation or a more long-term stabilisation to a peculiar set of environmental conditions.

5. Discussion

The stability of the spot-patterns in the Winchester, Ipswich and intervening populations of *M. jurtina*, accords well with our earlier and more widespread studies of first-order variation (Ford, 1965). Thus it seems that we are justified in concluding that in both sexes, spot-distribution is stabilised throughout the southern half of England from the east coast to west Devon

and that major deviations from the basic type occur rarely, if at all. Further west, the insect assumes an " East Cornish " form in which the spotting of the females is bimodal at 0 and 2 spots, the transition from the " Southern English " stabilisation being remarkably abrupt (Creed *et al.*, 1969).

A recent study of the stability of spot-distribution throughout the whole range of *Maniola jurtina*, (Dowdeswell and McWhirter, 1967) based on British Museum collections covering the years 1890-1935, has shown that the Southern English stabilisation does not end at the North Sea but extends at least to Finland, Bulgaria and Southern France, so constituting a " General European " stabilisation. Moreover, just as we find different stabilisations in Ireland, the West Country and the Isles of Scilly, so others occur in peripheral areas of southern Europe such as North and South Iberia, North-West Africa and Western Asia. All of these are areas where the species is approaching the limit of its range and spotting seems to be adjusted accordingly.

As the previous data have shown, a certain amount of second-order variation both inter- and intra-seasonal, occurs in the *jurtina* populations of southern England. This is in marked contrast with our findings for the rest of Europe where, even allowing for rather small samples, there appeared to be a much higher degree of homogeneity and a lack of second-order differences. In the southern English populations such variation in the males mainly affects the proportion of individuals with 2 spots, while in the females (with the notable exception of the population in Hatfield Forest) fluctuations occur at 0 and 2, the 1-spot value being relatively invariable and acting, as it were, as a pivot for those on either side. In general, intra-seasonal variation has taken the form of a reduction in spotting (judged by spot-average) in both sexes, being more pronounced in the female as the emergence progresses. It recurs irrespective of environmental changes. However, this pattern of change is by no means universal for in some populations, high spotting is a feature of the end of the season, not the beginning. Thus at Dunmere (Cornwall) in 1962, the spot-average of the early females was 1·22 while later it was 1·27.

The causes of second-order intra-seasonal variation have been investigated in some detail but the situation is still far from clear. From the results of extensive field sampling it seems certain that selection for characters controlled by spot-genes is predominantly endocyclic and takes place during the larval and pupal stages. This is only to be expected bearing in mind that the butterfly may spend as much as three-quarters of its life-cycle as a caterpillar. At one time it was thought that the Braconid parasite, *Apanteles tetricus* might play some part as a selective agent (Dowdeswell, 1961, 1962) but it now seems more likely that bacteria may exert a significant effect. As for inter-seasonal variation, a controlling factor may well be fluctuation in the weather from one season to the next, particularly temperature and humidity. This is an aspect at present under investigation and will be the subject of a separate paper.

6. Summary

1. Populations of the Meadow Brown butterfly, *Maniola jurtina*, in the vicinity of Winchester and Ipswich have been sampled regularly from 1961 to 1968. Periodic samples from intervening populations are also available.

2. During this period the general pattern of spot-distribution has remained remarkably stable.

3. Second-order spot-variation has occurred in all the populations studied, both inter- and intra-seasonal.

4. Intra-seasonal variation is characterised by a reduction in spotting as the season proceeds. This occurs irrespective of fluctuations in the environment.

5. The stability of spotting in the samples studied serves to confirm the concept of a " Southern English " stabilisation. This contrasts sharply with the " East Cornish " stabilisation further west. To the east and southwards, the " Southern English " stabilisation continues at least as far as Finland, Bulgaria and Southern France (" General European " stabilisation).

6. Bacteria may play a part in influencing intra-seasonal spot-variation. The effect of climatic change on inter-seasonal variation is being investigated.

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7. References

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