Temperature Effects on *Maniola jurtina* (L.) (Lep. Satyridae)

by GEORGE THOMSON F.R.E.S.

While it would be misleading to say that a great deal of fruitful research has been undertaken with livestock of the species, it is true that *Maniola jurtina* has featured fairly prominently in the breeding and rearing cages of those who partake of this time consuming activity. Most of the articles resulting from these 'experiments' have been devoted to expressing anguish at the difficulties of obtaining ova from the females or of bringing the young larvae through the precarious winter season, although a few have dabbled in minor genetic problems. The effects of temperature on the melanin pigments of the Pieridae and Nymphalidae as well as some moths are well known, but there is no record of such experiments on *jurtina* or any other Palaearctic Satyrid as far as I know. It has been suggested by those who are not familiar with the complex nature of the species that the occurrence of the known geographical phenotypes is the direct result of environmental conditions, particularly temperature, but, as was pointed out by Graves (1930) who probably knew the species better than any of his contemporaries.

"The theory that the Atlantic climate is the cause of the modification of *jurtina* in the direction of *hispulla* or of *hispulla* in the direction of *jurtina* is arguable, but it does not explain why maritime conditions produce such dissimilar results in Jersey and Brittany on the one hand and in the Scilly Isles on the other, or why the humidity of Cumbria and Merioneth has affected variation quite differently from the humidity of Tyrone".

This enigmatic situation could, in part, be explained in terms of selective forces working within rigidly isolated populations or population groups, and perhaps, in individual cases, as the result of the various remarkable phenomena which have been detected in the species—sympatric evolution (Ford, 1964) and temporal sub-speciation (Thomson, 1971). But unless the effects of environmental influences on the organism have been determined, the danger that data could be totally misinterpreted remains likely.

Key to Plate VII

Figures 1-12. *Maniola jurtina* ♀♀, experimental material: last larval instar and pupae kept at 30° C. Figures 1, 7 and 12 showing areas of wings in which scales have been detached during emergence (previously referred to f. *cinerea* Cosm.).

Figures 13-16. *Maniola jurtina* ♀♀, Dunblane, Perthshire, July 1972: collected in locality from which experimental material was obtained.

(Figures 1-7, 9-11: uppersides; 8-12, 16: undersides)

It was with this in mind that an attempt was made to resolve these problems. It is known that the critical period during which temperature has its effect on the resulting wing patterns is that of the late larval and early pupal stages. The use of swept larvae was, therefore, considered to be a satisfactory way of obtaining the livestock on which temperature experiments were to be carried out. It was hoped that a great number of these creatures would be obtained without too much trouble, but the experience of six nights work producing only twenty four larvae proved this to be rather optimistic in spite of the fact that expert advice on this method of collecting was kindly given by Mr W. H. Dowdeswell. The total sample was taken from one locality, a railway embankment in Dunblane where the species is common, and was collected over the period from May 21 until June 15 [May 21 (3), 27 (8), June 4 (7), 5 (4), and 15 (2)]. This was divided into two groups one of thirteen larvae which was to be reared through at a constant temperature of 30°C from the final larval instar, and the other into three sub-groups for periods of the first one, two and three weeks of the pupal stage at 6°C. The high temperature was maintained by a 100 watt electric light bulb enclosed within a one foot square metal box acting below the 'rearing box'. Fresh foodplant had to be supplied at least once a day, sometimes more often, as the heat quickly dessicated the grass. The low temperature group was kept in a domestic refridgerator. Both groups were kept in total darkness throughout the feeding period; even when foodplant was changed this was done in dark red light.

Larval/pupal period

High temperature: A remarkable acceleration of the growth rate was immediately noticed, the larvae feeding at gluttonous rate twenty four hours a day. Two of the fifteen larvae died as larvae and a further three as pupae. Larval size varied a great deal, but many pupated when still relatively small. Pupation took place between June 2 and 25 [June 2 (4), 3 (1), 5 (2), 8 (1), 12 (1), 19 (1), 23 (1) and 25 (1)]. Pupal markings varied considerably but they seemed to be far more lightly marked on average than those illustrated in the available literature or in that most eloquent description by Newman (1874).

"The colour of the chrysalis is pale apple-green, freckled with whitish or yellowish green, and adorned with purple-black markings, of which the more conspicuous are first, two dorsal series, commencing behind the head, passing on the fourth, seventh, eight and ninth segments, and continuous on the remainder; secondly, a series passing over the ears, and occupying the dorsal margin of the wing cases; thirdly, an angulated longitudinal stripe on the wing cases, dividing them into two nearly equal parts; fourthly, a shorter stripe nearer the tip of the wing cases; and fifthly, the cases of the fore and middle legs."

The only one of the markings described above which was conspicuously present in all of the pupae was the 'angulated longitudinal stripe', the remainder of the markings being more or less obscure. There was no correlation, however, between pupal markings and those of the imagines. The emergence began on June 11 and continued until July 3, and on the fol lowing dates: June 11 (1 with a further 2 dissected from the pupae), 14 (1), 19 (1), 24 (2), 30 (1), July 1 (1) and 3 (1). All the butterflies were female except a single male dissected on June 11. The period spent in the pupae ranged from seven to sixteen days, averaging 10.8 days, which represents between a half and one third of the period normally spent in the stage. Those which emerged later tended to have been those which had remained in the pupae longer, but not to a significant degree.

Low temperature: The larvae were initially placed at 6°C but when the fully grown larvae became totally inactive it was realised that pupation was not likely at that temperature and were placed at room temperature. By this time they had become appreciably larger than those kept at the high temperature. Pupation took place on July 11 (1), 12 (1), 13 (2), 20 (1), 21 (2), 23 (1), and 25 (1)., immediately after which they were returned to the refridgerator. Their colour varied a great deal tending to be rather lightly marked as was the case with the high temperature group. It was presumed that this divergence from the norm was due to local or geographical variation and not temperature. All of the nine pupae died within a short time of being removed from the refridgerator.

Comparison of the imagines

Because of the 100% mortality in the low temperature sample, the females reared at 30°C had to be compared with a series from the emergence in the same year (1972) and locality from which the larvae had been swept. Although it would be impossible to find out exactly what were the prevailing conditions in the locality during the late larval and pupal stages, it is certain that the temperature during that period never exceeded 20°C. During the period from the end of May. until the middle of July, when the *jurtina* from which the sample was taken would have been in these early stages, the temperature range was about 7°-13° (night) and 12°-20° (day). It would be safe to say, therefore, that the 'wild' sample lived through considerably colder conditions than those reared artificially. The species emerged in the locality on the July 13 and was on the wing until September 5. This was a week or so later than is usual in the area, but the spring and early summer had been remarkably unseasonal.

The upperside fulvous markings of the wings were modified by the high temperature, but only within certain limits. The length of the submarginal fulvous band on both fore and hindwings was unchanged (i.e. the total number of interspaces in which the colouring is present). However, in all of the reared specimens the ground colour invaded the fulvous in one or more of the following ways:

a) as a suffusion of the dark scales of the ground colour (f. *huenei* Krul.)

b) by an encroachment of the ground colour along the nervures.

c) by reducing the width of the fulvous band, usually by an increase in the width of the outer margin.

Two of the specimens were rather small with a wingspan of only 43 mm and 46 mm compared to the average for the locality of about 52 mm. Effects other than these were not pronounced although there was an indication that the size of the apical eyespot and the intensity of the underside dark medial line and outer margin of the forewings were increased, but more material would be required to confirm this.

Three of the individuals had the appearance of an 'albino' type which is encountered more or less frequently in many parts of Britain and Central Europe and which, until now, I have placed under the name of f. *cinerea* Cosm. These forms are often reported to have scales which are malformed, lying at odd angles or totally lacking in some parts of the wing. The fact that three of the specimens resulting from temperature experiments were affected in this way one of them also lacking a great number of scales on the underside, seemed to be more than coincidence. Examination of the empty pupal cases of these individuals revealed that the missing scales were still adhering to the inner surfaces. Undoubtedly, the high temperature and consequential low humidity prevented the wing membrane from effecting a normal release. The scale malformation can thus be explained simply as a result of dessication, and the many published notes attributing this aberration to disease are shown to be misguided. It should be pointed out, however, that all the specimens which go under the name of f. *cinerea* are not due to improper emergence and reference to the relevant literature (Thomson, 1969) will assist in the identification of this form.

Ford (1945) and others have reported that a high temperature tends to restrict melanin production and a low one promote it. The results of experiments on *Aglais urticae* (L). are well known. The situation is reversed in the *Pieris* species and, as the brown colour in *jurtina* is, presumably, a melanin, this is also the case in this species and related Satyrids.

Temperature effects in wild populations

The effect of temperature on the wing markings of the species must be insignificant compared to its genetic make up, particularly if we consider the fact that these races which are more brightly marked with fulvous in the south of Europe must be subjected to considerably higher temperatures than those of central Europe. The subspecies *hispulla* Esper of

Spain and *jurtina* of North Africa differ from the races found further north, in France and Britain, to a greater extent than from each other. However, the modification of the fulvous in ssp. *jurtina* (and f. *fortunata* Alpheraky from the Canary Islands) in relation to that of *hispulla* (with its typically unbroken submarginal fulvous band) could well be largely environmental as they show the same tendencies which have been seen in the experimental material. The narrowing of the rather distinctive fulvous band of the individuals from the late emergence on the Isle of Wight (Thomson, *loc. cit.*) and parts of southern Europe could also be due to temperature alone but there are great dangers in drawing any conclusion in this field as many of the late emerging specimens could well be appearing at a much later date because of cool conditions prevailing in the early stages. The rather brightly marked females from south-east Sweden could well be the result of cooler conditions in the north than those to which ssp. *janira* of Germany are subjected.

Perhaps the best illustration of the temperature effect on the wing markings of other Satyrid species in the wild can be seen in the British *Pararge aegeria* (L.) This butterfly is interesting in that it passes the winter either as larvae or pupae. Those which 'hibernate' in the pupae, and thus in the relatively cool conditions of our winter, emerge in April, while those which winter as larvae pupate in spring and produce a brood in May and early June. The individuals of Generation I, part 1 (as termed by Ford) are much more extensively marked with fulvous than the specimens from Generation I, part 2. It is likely that all of the first brood *aegeria* from the west of Scotland pass the winter as larvae as they do not emerge until the end of May, thus passing through the pupal stage in spring. The markings of these butterflies are almost as light as the Generation I, part 1 specimens from the south of England; in some cases more so, reflecting the effect of the cooler conditions in the northern part of Britain. It is notable that the typical *aegeria* from southern Europe is, like *jurtina,* more extensively marked with fulvous than its northern counterpart, indicating, perhaps, a strong physiological as well as evolutionary relationship.

The total mortality of the low temperature sample, although disappointing, is interesting as it could suggest the limits to which the species can be subjected and, consequently, the reason for the range of the species in northern Europe and in the mountains. *Jurtina* does not fly much further north than 62° in Scandinavia although it is found in the Norwegian valleys a little further north. The species is not commonly found in places above about 1,000 metres in Central Europe and 1,500 metres in southern Europe. There are some notable exceptions to this, particularly the colony at Verbier in the Swiss Valais where the butterfly can be taken commonly at 1,750 metres. The inability of this insect to withstand seven days at a temperature of 6° would strictly limit the northern and altitude distribution of *jurtina* and there is every possibility that it would do so to something very close to that which we find to-day.

Because of the inadequate numbers involved in this study, a few female *jurtina* were set to lay during the summer. Some 500 eggs were obtained. An attempt was made to force the hatching of 50 of the ova by placing them at 20°C but all died within a day. A similar fate met 50 first instar larvae which were treated likewise, and it was concluded that the remaining stock would not be exposed to high temperatures until they had reached at least the fourth instar. This would seem to show that the immature stages of this species are very intolerant of temperature excesses, whether they be high or low, which is remarkable when we consider the very wide distribution of the butterfly.

Conclusions

1. Temperatures of 6°-30° C maintained throughout the last larval instar and pupal stages had no effect on the pupal markings of *Maniola jurtina.*
2. A low temperature of 6° C prolonged the larval stage and encouraged the development of larger than normal larvae, but placed at this temperature for only seven days at the pupal stage created a 100% mortality.
3. A temperature of 30° C reduced the pupal stage to between one-half and one-third of the normal period, and reduced the fulvous markings on the upperside of the forewings and hindwings, but only within certain genetically determined limits. There was also an indication that the size of the apical eyespot was increased and the medial line on the underside of the forewings darkened, but not greatly or consistently.
4. While the effects of temperature can be seen in wild populations, the factors producing the known phenotypes of the geographical races are genetic and not environmental.
5. The northern and altitude limit of the species is possibly determined by the inability of the pupae to withstand low temperatures for periods as short as a few days.
6. The form *huenei* Krul. is directly, and the form *cinerea* Cosm. is indirectly the result of unusually high temperatures during the immature stages.

REFERENCES

Ford, E. B. (1945). *Butterflies*, New Naturalist Series, London: 240-244.

———, (1964). *Ecological Genetics*, London.

Graves, P. P. (1930). *Entomologist*, **63**: 79-80.

Newman, E. (1874). *The Illustrated Natural History of British Butterflies and Moths*, London: 92-93.

Thomson, G. (1969). *Ent. Record*, **81**: 10-11, 116.

———, (1971). *Ent. Record*. **83**: 87-90.

Backcroft, Dunblane, Perthshire, FK15 0BL.

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