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The evolutionary significance of bimodal emergence in the butterfly, *Maniola jurtina* (Lepidoptera: Satyrinae) (L.).

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Most temperate butterflies exhibit a tightly synchronized unimodal adult emergence to facilitate mate location. Exceptions are presumably subject to unusual selection pressure. This study examines the pattern of emergence in *Maniola jurtina*, which was found to exhibit both unimodal and bimodal emergence patterns at different sites in south-east England. The bimodal pattern was found on chalk grassland; elsewhere the emergence was unimodal. Adults from each emergence peak rarely meet, suggesting that there may be some degree of reproductive isolation. Morphological measurements and electrophoretic analysis of allozyme frequencies are carried out to quantify differentiation between emergence peaks. Captive stock was reared to examine differences in the immature stages. Butterflies from each emergence differ significantly in most morphological variables measured, those from the second peak tending to be smaller. The immature stages differ in morphology and longevity of the egg stage. Allozyme frequencies did not differ between peaks, suggesting that they are not reproductively isolated. Explanations for the maintenance of differences between emergence peaks despite gene flow are discussed. I propose that division of offspring between two emergence times may have evolved to avoid the risk inherent in placing all offspring in one peak which may be rendered inviable by temporal fluctuations in habitat quality.

ADDITIONAL KEY WORDS:—Polymodal emergence – variation – electrophoresis.

CONTENTS

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INTRODUCTION

An organism with discrete generations must, to breed successfully, time its reproductive stage to coincide with that of conspecifics. The accuracy of timing required is dependent upon the longevity of this stage: if it is short then there is little leeway for error. The result is that most ephemeral organisms, particularly insects, exhibit a tightly synchronized unimodal emergence curve (Waldbauer, 1978). A further refinement is that males frequently emerge slightly earlier than females, a phenomenon known as protandry (Scott, 1977; Wiklund & Fagerstrom, 1977). This maximizes the number of unmated females which a male is likely to encounter in its lifetime, a process which has been mathematically modelled with some success by Wiklund & Fagerstrom (1977) and Iwasa *et al.* (1983).

Along a latitudinal gradient, the regulation of emergence timing must vary such that local populations are maintained in appropriate synchrony with their environment (Beck, 1968; Tauber & Tauber, 1976).

The generality of synchronized emergence renders exceptions particularly interesting, for presumably unusual and powerful selection pressures are in operation. Records of polymodal emergence patterns are rare, although this may be because they are difficult to distinguish from multivoltine patterns in wild populations. A compilation of published records is shown in Table 1. The significance of these patterns has not been established in any species. Dennis (1971) suggested that a bimodal pattern could be established as a result of selection against individuals emerging in the middle of the emergence period, and eventually produce total reproductive isolation of the modes. Such selection would have to be extremely strong to overcome the swamping effect of cross-breeding between modes (Lewontin, 1974).

On several occasions a bimodal emergence pattern has been observed in *M. jurtina* (Dowdeswell, 1961; Thomson, 1971; Brakefield, 1982; Shreeve, 1989). As yet no satisfactory explanation has been proposed. In this study I quantify morphological and allozyme frequency differentiation between peaks of the bimodal emergence, and examine how variation in emergence timing may be maintained. Conclusions are sought as to the evolutionary origins of this phenomenon.

MATERIALS AND METHODS

Emergence patterns

To provide a measure of the temporal distribution of emergence of *M. jurtina*, estimates were made of the population density of adult insects at 2–3 day intervals throughout the flight period in 1989. This was carried out at Aston Rowant N.N.R. (N.G.R. SP724958), an area of chalk grassland in the Chiltern hills, and at Bernwood Forest (N.G.R. SP612104), a lowland woodland on clay soil (Fig. 1). Sampling was continued at Aston Rowant in 1990. These sites were chosen as the butterfly was known to exhibit a bimodal emergence at Aston Rowant and a unimodal one in Bernwood Forest (T. Shreeve, personal communication). Estimates were made using the number of butterflies caught per hour when hand netting. The entire area of suitable habitat was searched at

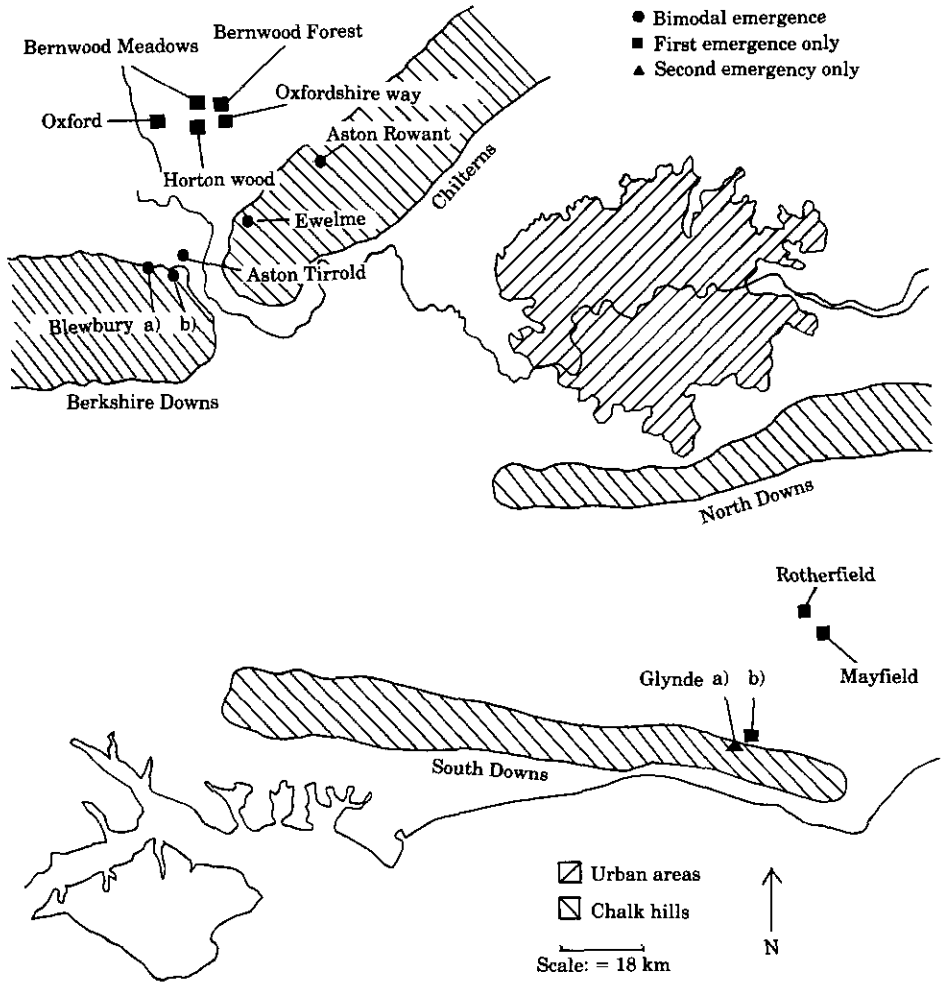

Figure 1. Study sites, showing pattern of emergence exhibited. # = Bimodal emergence, * = first emergence only, 0 = second emergence only.

each visit so that microdistribution changes did not have a major effect upon the estimated population density. This technique is highly dependent upon weather conditions, as this affects the activity, and hence apparency, of the butterflies. Fortunately in 1989 and 1990 there were numerous days in which conditions

TABLE 1. Examples of polymodal emergence patterns in insects

Species	Emergence pattern(s)	Area	Source
Callosamia promethea (Lep.)	Unimodal, trimodal	Illinois	Waldbauer (1978)
Chaoborus americanus (Dip.)	Bimodal	Michigan	Bradshaw (1973)
Chloridea obsoleta (Lep.)	Bimodal	Caucasus	Danilevski (1965)
Eurytides marcellus (Lep.)	Bimodal	U.S.A.	Waldbauer (1978)
Hyalophora cecropia (Lep.)	Bimodal	Illinois	Sternberg & Waldbauer (1969)
Manduca sexta (Lep.)	Bimodal	N. Carolina	Rabb (1966)
Maniola jurtina	Unimodal, bimodal	S.E. England	Present study
Papilio glaucus (Lep.)	Unimodal, bimodal	New York State	Hagen & Lederhouse (1985)
Rhagoletis pomonella (Lep.)	Unimodal, bimodal	Wisconsin	Oatman (1964)

were warm and dry and judged to be more or less optimal for butterfly activity, justifying comparisons between days. Catch per unit time was used in preference to the more usual mark–recapture method which is not possible with large populations, and which is subject to bias as handling may affect behaviour.

Removal of samples from each site inevitably reduced capture rate on subsequent days. However, the populations were sufficiently large that this source of error was unlikely to greatly alter the pattern of emergence.

Adult morphology

Continuous sampling of adult butterflies at Aston Rowant at two to three day intervals provided material for characterization of morphological differences between butterflies according to their emergence date. In total 278 male and 225 female butterflies were captured. Thirteen morphological variables were measured. Choice of attributes for measurement was based upon two factors: whether they could be seen to vary in the field, and whether they were measurable given the equipment and techniques available.

The measurements made were:

(a) Number and area of spots on the underside of the hindwing, measured using image analysis. Any spots visible to the unaided eye were scored, the method used by Brakefield (1982, 1984) to enable comparisons with his research. The earlier work of E. B. Ford and co-workers (Dowdeswell, 1981) ignored spots below a certain size, but a more recent study comparing the two methods (Brakefield & Dowdeswell, 1985) indicated that relative differences between samples remain the same whichever method is used.

(b) Wing damage. The number of tears visible to the naked eye in each wing margin were counted. This was carried out as it provides an indication of the age of a butterfly. A separate total was kept for damage which was likely to be the result of bird attacks (see Owen & Smith, 1990 for details of beak mark recognition), but such damage was founds to be rare in the populations sampled.

(c) Wing length, from the base to the tip of the forewing.

(d) Wing area, measured using image analysis. This was measured to enable calculation of wing loading (wing area/weight), as this may have important effects upon an individuals ability to fly, as shown by Danthanarayana (1976).

(e) Dimensions of genitalia in males. The tip of the male abdomen was first softened by soaking overnight in 10% NaOH. The genitalia were then teased from the surrounding tissue and soaked overnight in absolute alcohol to dehydrate, and thus render transparent any remaining tissue. The genitalia were then mounted in Euparal under a cover slip on a number slide. The length of the valves, their maximum and minimum widths and the length of the penis were recorded. These measurements were used in preference to Thomson's (1973) *F* value, as this was found to be subjective, and entirely inapplicable to certain rare valve shapes. Measurement of maximum and minimum widths was carried out to give some indication of the height of the dorsal process, one of the most variable aspects of valve shape.

Morphology and life-cycle timing in captivity

Butterflies were reared in captivity to examine how the timing of the life cycle differed according to emergence time of the adult butterfly. This also enabled a

morphological study of the immature stages. To obtain stock, wild caught females from Aston Rowant and Bernwood Forest were placed in translucent sandwich boxes approximately 8 × 8 × 5 cm. A small quantity of grass, and tissue paper soaked in 10% sucrose solution was provided. The box was placed under fluorescent lighting at a constant temperature of 26°C. Oviposition almost invariably occurred, although the number of eggs laid was low, never more than 60 per female.

The eggs were kept at 26°C until they hatched. The larvae were then transferred to potted grass or clear plastic pots containing cut grass, both of which were kept in an unheated outhouse under natural lighting. They remained in these conditions throughout the following winter and spring. At each stage of development drawings were made to record morphology.

Exceptionally high mortality during the winter prevented rearing of sufficient numbers to examine adult emergence timing.

Starch gel electrophoresis

In 1990 sampling was also carried out at 14 sites (Fig. 1), both lowland and chalk grassland, to assess the extent of the bimodal emergence and to provide material for electrophoresis. Sample sizes are given in Table 2. At six of these sites the emergence was bimodal. At Aston Rowant and Glynde samples were taken from both peaks. Sampling was only carried out during the second emergence peak at the remaining four bimodal sites. All samples taken in 1990 were used for electrophoresis. Butterfly abdomens were removed and stored for one to five months at −70°C until electrophoresis could be carried out.

Sample preparation

Each specimen was placed in a numbered centrifuge tube to which 0.3 ml of extraction buffer (Pasteur *et al.*, 1988) and a few grains of purified sand were added. They were then ground up using a glass rod driven by an electric drill.

Electrophoretic procedures

Proteins were separated using horizontal starch gel electrophoresis following the method described by Pasteur *et al.* (1988). Starch was obtained from the Sigma Chemical Co. and used at a concentration of 25.5 g per 230 ml of gel buffer. The two most suitable buffer systems proved to be continuous Tris-citrate at pH 8 (Ahmad, Skibinski & Beardmore, 1977) and discontinuous citrate histidine at pH 7 (Shaw & Prasad, 1970). Gels were run at 60 mA for 4.5 hours.

Enzyme staining protocols are given in Pasteur *et al.* (1988). Twelve enzymes were resolved, of which four proved to be polymorphic and were sufficiently clear to screen routinely: phosphoglucose mutase (PGM), phosphoglucose isomerase (PGI), isocitrate dehydrogenase 1 (IDH-1) and isocitrate dehydrogenase 2 (IDH-2). Leucyl-amino peptidase (LAP), and malic enzyme (ME) were also polymorphic but could not be resolved sufficiently clearly to allow accurate interpretation.

Malate dehydrogenase, glucose-6-phosphate dehydrogenase, adenylate kynase, aldolase and glyceraldehyde phosphate dehydrogenase were resolved and found to be monomorphic in all samples analysed.

Allozyme travel was scored as a percentage of the distance travelled by the

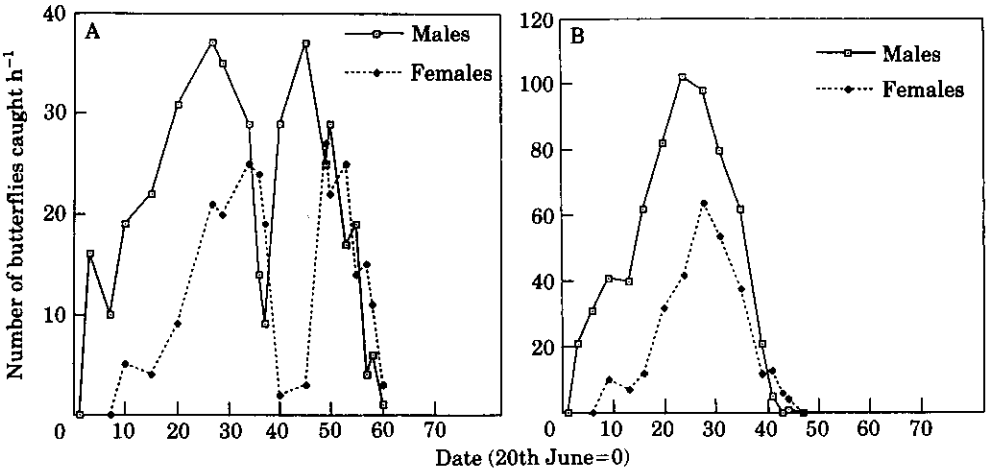

Figure 2. Changes in population density (estimated from capture rate per hour) with data. A, Aston Rowant; B, Bernwood Meadows.

most common allozyme, the most usual method of gel interpretation (Pasteur *et al.*, 1988). Allele frequencies for the four polymorphic enzyme loci are given in Appendix 1.

Analysis of the data was carried out using BIOSYS-1, a program which carries out most commonly used analyses of electrophoretically detectable variation. *F*-Statistics (Wright, 1940, 1943, 1951) were chosen from the large number of measures of genetic variability available as they have been used in most recent studies upon the Lepidoptera, enabling comparisons to be made. Calculation of *F*-statistics treats all samples as subsets of a single population, and produces measures of the deviation from Hardy-Weinberg equilibrium within the population (F_{IT}), deviation from Hardy-Weinberg within subsets (F_{IS}) and the degree of genetic differentiation between subsets (F_{ST}).

In 1990, female butterflies, after egg-laying, were frozen at −70°C for electrophoresis. The larvae were then reared and used as electrophoretic material to enable a check to be made on the validity of gel interpretation by comparison of parental and larval phenotype.

RESULTS

Timing of the adult flight period

Numbers of butterflies caught per hour against date is shown for 1989 in Fig. 2 for Aston Rowant and Bernwood Meadows. A bimodal emergence curve is evident at Aston Rowant, which does not occur at Bernwood Meadows. The trough is not the result of poor weather as warm dry weather prevailed throughout the flight season. The onset of emergence occurs at approximately the same time at all sites. In both 1989 and 1990 this was abnormally early due to the unusually warm springs. The first butterfly was recorded on 14 June in 1989 and 30 May in 1990 (examination of the extensive collection at the Hope Entomological Museum suggests that this may be the earliest record of this species in Britain).

At all sites the first males were recorded 3–6 days before the first females, as is usual in univoltine butterflies (Wiklund & Fagerstrom, 1977). Numbers of

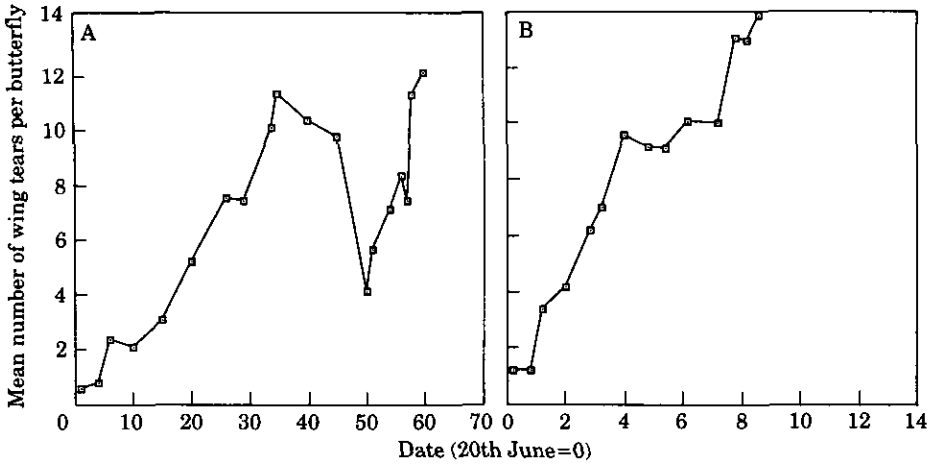

Figure 3. Changes in population age structure during the 1989 flight season as measured by wing wear. A, Aston Rowan; B, Bernwood Meadows (sexes combined).

butterflies on the wing peaked at all sites *c.* 1 month after the first emergence, and subsequently declined. Excluding a few sites on chalk this decline continued until the flight season ended *c.* 2 months after the first emergence: between 4 and 7 August in 1989.

At Aston Rowant newly emerged specimens appeared in the population during the tail end of the first flight period, during the last week of July. These could be identified by their pristine condition, and in very fresh specimens by their soft wings. In addition mating pairs were found. As females mate only once soon after emergence (Svard & Wiklund, 1989; Goulson, 1991) this indicates that they were newly emerged. Numbers in the field reached a second peak *c.* 2 weeks after the initiation of this second emergence, between 5 and 10 August in 1989, and subsequently declined until the last capture on the 23 August. Confirmation that the apparent trough at Aston Rowant is not due to dispersal of butterflies from the site is provided by changes in wing wear during the season (an indicator of butterfly age) (Fig. 3). The population age structure shows a distinct trough at Aston Rowant corresponding to the flush of emergence of new butterflies.

The patterns of emergence and wing wear were reported in 1990, with timing advanced by *c.* 1 week. Second emergences, in which butterflies were present in good numbers after their disappearance at non-chalk sites, were identified along the Ridgeway in Berkshire, in the Chilterns, and on the South Downs near Brighton (Fig. 1).

At the South Downs site on exposed chalk grassland no butterflies could be found during the first emergence. Butterflies were found, and a sample taken, *c.* 500 m away on pasture in the valley floor. Generally butterflies were scarce at all chalk grassland sites during the first emergence in 1990.

Morphological differences between emergence peaks

The mean and standard deviation of each variable measured for first and second emergence groups in 1989 is shown in Table 2. Butterflies captured

TABLE 2. Differences in selected morphological variables between first and second emergence peaks of *Maniola jurtina* (1989, Aston Rowant)

	First emergence			Second emergence			
	X	σ	N	X	σ	N	P
Males							
Hindwing spot number	2.19	0.84	104	2.03	0.55	134	0.072
Hindwing spot area (mm^2)	37.0	26.9	104	35.0	23.5	134	0.557
Wing area (mm^2)	709	58.8	123	676	68.7	154	0.000
Wing length (mm)	24.5	0.920	123	24.0	0.822	154	0.000
Number of wing tears	4.56	5.34	123	5.09	4.08	154	0.350
Valve length ($mm \times 10^{-1}$)	63.8	2.96	123	62.4	3.15	98	0.001
Valve width (max) ($mm \times 10^{-1}$)	29.1	2.01	123	28.6	2.04	98	0.060
Valve width (min) ($mm \times 10^{-1}$)	23.3	1.62	123	23.2	1.46	98	0.820
Penis length (mm)	49.7	3.45	111	49.2	3.58	94	0.282
Females							
Hingwing spot number	0.438	0.681	48	0.222	0.526	99	0.037
Hingwing spot area (mm^2)	4.71	8.15	47	1.93	4.53	99	0.009
Area (mm^2)	862	86.5	50	775	72.3	102	0.000
Wing length (mm)	26.5	0.990	52	26.1	0.793	103	0.003
Number of wing tears	6.29	5.24	52	6.38	5.44	103	0.922

t-test used to test for differences between emergence peaks.

during the overlap between emergences were excluded from the analysis. A *t*-test is carried out for each variable to test whether emergences differ. The two emergence groups differ significantly in the majority of morphological variables measured, and in both sexes. The principle differences are in measures of size. Butterflies of the second emergence were generally smaller and lighter, had a lower wing loading, and fewer spots. However, the degree of variation within each emergence peak is such that no single morphological attribute can be used to identify to which peak an individual belongs. Differences in valve shape between emergencies, as described by Shreeve (1989), were not found.

Differences between the immature stages

Eggs obtained from females from the two emergence peaks were reared, and the timing and morphology of each stage of the life cycle recorded. Two differences were found:

Morphology of the egg. Eggs of *M. jurtina* are approximately spherical, and possess a number of vertical keels. The mean number of keels differed between emergence peaks. Eggs from the first emergence had 16–18 keels (mean = 17.3, $\sigma = 0.99$, $N = 22$ for Aston Rowant, mean = 17.5, $\sigma = 0.62$, $N = 27$ for Brenwood Forest). Those from the second emergence at Aston Rowant had 18–21 keels (mean = 20.2, $\sigma = 1.2$, $N = 25$). This difference between emergencies is significant (*t*-test, $P < 0.001$).

Timing of egg hatching. Egg were kept at a constant 26°C in a controlled environment. Those obtained from Bernwood Forest and from the first emergence at Aston Rowant hatched after 8–16 days. Those from the second emergence at Aston Rowant emerged after 18–25 days. A statistical test cannot be carried out as eggs were not removed from each female daily and kept separately: the precise duration before hatching was not recorded for each egg.

TABLE 3. Summary of Wright's F-statistics at all loci

Locus	F_{IS}	F_{IT}	F_{ST}
PGM	0.025	0.005	0.019
PGI	0.012	0.002	0.014
IDH-1	0.026	0.070	0.046
IDH-2	0.059	0.029	0.028
Mean	0.013	0.010	0.023

Gene flow between emergences

The flight timing of the two emergence peaks indicates that there is limited potential for gene flow between peaks within a flight season. The only substantial overlap is between old females of the first emergence and newly emerged males of the second. However, as females mate only once soon after emergence it is unlikely that cross-fertilization between emergence peaks occurs.

The mean value for F_{ST} of 0.023 indicates that very little genetic divergence has occurred, as only 2.3% of the variation present in allele frequency was due to between-site variation (Table 3). To analyse what proportion of this differentiation was due to isolation of the two emergencies, a hierarchical analysis of population differentiation was carried out. This partitions total differentiation into differentiation between and within emergences. The mean value of $F_{(\text{emergence-total})} = 0.001$ indicates that only 0.1% of the total observed variation was due to divergence between emergences: the population is effectively panmictic.

DISCUSSION

The results presented above are somewhat paradoxical, for there are two apparently contradictory lines of evidence:

(a) The appearance of a distinct second emergence of *M. jurtina* at some sites in south east England is beyond doubt. A number of lines of evidence rule out a second generation as the cause of the second emergence. It is unlikely that there is sufficient time for development of larvae between emergences. Butterflies have been studied and bred in captivity for many years. A second generation has never been recorded in *M. jurtina*, even in southern Europe. All larvae reared in this study developed extremely slowly, reaching only the second instar before hibernation.

These bimodal populations were found only on chalk grassland and scrub. There was little potential for cross-breeding between emergences in either of the study years, and there is reason to believe that during typically cooler British summers the two emergences are widely separated in time, the second emergence appearing at least a month after the first has disappeared (Shreeve, 1989).

A number of differences were observed in both adult and immature stages between emergence peaks. Some, such as differences in adult size, may be explained by environmental effects such as changes in food quality towards the end of larval growth. Others would seem unlikely to be due to environmental effects, particularly differences in the immature stages under controlled conditions, such as differences in the duration of the egg stage.

(b) The electrophoretic study demonstrates that isolation of emergences has not occurred, as genetic divergence is neglible.

A number of questions arise as a result of this contradiction:

(a) How is gene flow occurring if the adults rarely, if ever, meet?

(b) How is bimodality maintained despite gene flow? Similarly, how are differences in morphology between emergences maintained, such as the number of keels on the eggs?

(c) What is the adaptive significance of variable emergence timing?

The first question is the most simple to answer. Although there is little potential for adults of different emergences to meet and mate within one generation, if each emergence peak does not breed true then the adults in each emergence peak will be of mixed parentage, and cross-breeding will occur. Waldbauer (1978) describes such a situation in the robin moth, *Hyalophora cecropia* which exhibits bimodal emergence. He showed that although emergences do not breed true in this species, it is clearly under genetic control, for artificial selection could dramatically change the proportions of offspring in each peak.

The second question, as to how bimodality is maintained despite gene flow, is more difficult to answer. Why the two peaks do not merge due to the swamping effect of interbreeding is unknown. A bimodal emergence could theoretically be produced by an interaction between environment and genotype. For example, if larval size has not reached a critical threshold by a certain time of year (perhaps controlled by daylength) then the pupal phase may be extended by several days. Therefore larvae which mature later would also spend longer as pupae and so emerge as adults several weeks after fast developing larvae. Clearly more research is required to elucidate the mechanisms which control emergence.

Differences between emergences such as egg morphology and duration may be due to variable expression of the genotype according to emergence time. Whatever cues are responsible for delaying emergence may also trigger expression of alternative gene complexes (Jones, Rienks & Wilson, 1985). A comparable situation is found in many tropical butterflies which exhibit dry and wet season polyphenism, such as *Melanitis leda* (Brakefield, 1987).

Phenotypic changes according to emergence time are by no means unique to *M. jurtina*. They have been recorded in a number of polymodal species, such as the zebra swallowtail, *Eurytides marcellus* (Scudder, 1889), and the phantom midge, *Chaoborus americanus* (Bradshaw, 1973).

An answer to the third question, as to what is the adaptive significance of bimodal emergence timing, must be speculative. A possible explanation is provided by the study of other insects with polymodal emergence. A recurrent theme in such studies is that there is a latitudinal gradient associated with emergence patterns. Commonly emergence is unimodal in the higher latitudes of a species range, becoming polymodal in warmer climates. Examples include the moth *Callosamia promethea* (Waldbauer, 1978), and the tiger swallowtail, *Papilio glaucus* (Hagen & Lederhouse, 1985). At still lower latitudes both species become multivoltine. In accordance with this study Hagen & Lederhouse found no genetic differentiation between modes in polymodal regions.

Waldbauer & Sternberg (1973) likened the adaptive strategy involved in polymodal emergence to the metaphor which warns against putting all of the eggs in one basket. Polymodal emergence avoids placing all progeny in one 'temporal basket' in the following growing season during the critical period

encompassing adult development, emergence and reproduction. Partitioning the progeny between an early and a late emergence might allow at least some of the progeny of a pair to escape various detrimental factors which may occur at different times of the year, but that do not occur every year or vary in severity from year to year. This argument is supported by the latitudinal changes in modality of emergence described above, and by the work of Bradshaw (1973). He found that the early emerging morph of the phantom midge, *Chaoborus americanus* was at a selective advantage in a year when spring was early and the weather became continuously warmer. Conversely, in years when an early thaw was followed by refreezing of the pond, few early emergers survived, while late emergers flourished.

Maniola jurtina differs from other known examples of species with polymodal emergence in that the strategy varies with habitat type within a relatively small geographic area. However, the same principles may apply. The combined effect of later adult emergence and a prolonged egg stage is such that larvae from second emergence adults hatch over a month after larvae from first emergence adults. Brakefield (1982) reported low (first emergence) adult numbers of *M. jurtina* in 1977 which he interpreted as due to high larval mortality during the hot and dry preceding summer. In this study adult numbers in the first emergence at sites upon chalk were far higher during 1989 following the relatively cool summer of 1988, than during 1990 following the hot summer of 1989. Waldbauer (1978) suggested that polymodal emergence is generally associated with marginal areas where conditions tend to vary unpredictably from year to year. It is arguable that chalk grassland is a less predictable habitat than lowland meadow and open woodland, the other habitats occupied by *M. jurtina*. It is certainly more exposed to extremes of temperature, and to higher wind speeds and consequently may stress the water relations of both plants and animals. Larval foodplant (various grasses) may not be available during the summer months in dry years, causing high mortality of larvae from the first emergence, which hatch in August. Larvae from the second emergence, on the other hand, hatch in September or later. As the weather in the autumn is generally wetter and cooler, they are less likely to experience either water stress or a shortage of fresh grass. A possible counterbalancing advantage of early emergence is that the larvae have longer to feed and grow before hibernation.

An interesting comparison can be made with the strategy of *M. jurtina* in Italy, where the summers are hotter and drier than in England (Scali, 1971). Both sexes emerge in April and May and mate. The males then die, while the females aestivate for several months until September when they become active again and lay their eggs. This strategy, and that found on chalk grassland presumably provide alternative means of bridging a period of time during the hottest part of the year when conditions are unfavourable.

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APPENDIX 1

Frequencies of the two most common alleles at the four polymorphic loci studied, PGM, PGI, IDH-1 and IDH-2

	PGM		PGI		IDH-1		IDH-2		*n*
Bernwood meadows	0.795	0.151	0.823	0.069	0.895	0.105	0.956	0.044	139
Mayfield	0.733	0.200	0.793	0.069	*	*	0.897	0.103	30
Glynde (a)	0.841	0.114	0.857	0.071	0.864	0.136	1.000	0.000	22
Oxfordshire Way	0.829	0.092	0.865	0.014	0.838	0.149	0.986	0.014	38
Aston Rowant (a)	0.729	0.219	0.853	0.052	0.885	0.115	0.943	0.047	96
Bernwood Forest	0.897	0.086	0.800	0.083	0.870	0.130	0.967	0.033	29
Horton Wood	0.806	0.129	0.883	0.067	0.833	0.167	0.964	0.018	31
Oxford	0.759	0.148	0.864	0.091	1.000	0.000	0.955	0.000	27
Rotherfield	0.750	0.096	0.839	0.071	0.981	0.019	0.944	0.019	26
Aston Tirrold	0.914	0.034	0.759	0.121	0.875	0.125	0.982	0.018	29
Blewbury (a)	0.853	0.069	0.867	0.051	0.918	0.082	0.922	0.069	51
Blewbury (b)	0.738	0.214	0.783	0.043	0.804	0.196	1.000	0.000	21
Glynde (b)	0.800	0.129	0.900	0.057	*	*	0.971	0.029	35
Ewelme	0.717	0.150	0.783	0.117	0.942	0.058	1.000	0.000	30
Aston Rowant (b)	0.754	0.153	0.822	0.102	0.860	0.140	0.992	0.008	59