

Uniformity of wing spotting of *Maniola jurtina* (L.) in relation to environmental heterogeneity (Lepidoptera : Satyrinae)

T. G. SHREEVE*, R. L. H. DENNIS** & W. R. WILLIAMS***

*School of Biological & Molecular Sciences, Oxford Brookes University, Headington, Oxford OX3 0BP, U.K.

**Department of Biological Sciences, Keele University, Staffordshire ST5 5BG, U.K.

***Computing Service, Science Laboratories, University of Durham, South Road, Durham DH1 3LE, U.K.

Summary

Ventral hindwing spotting and wingspan of the meadow brown butterfly *Maniola jurtina* (L.) were measured on samples collected from 10 sites in North Wales which differ in climate, geology and habitat structure, known to produce significant diversity in another satyrine butterfly *Hipparchia semele* (L.). For both sexes of *Maniola jurtina* spotting was uniform over all sites, but size differed significantly. These results do not conform to models which relate hindwing spotting to weather or to habitat related activity differences and selection. Data on movements from another location, Brereton Heath, Cheshire, are used to suggest that the observed uniformity of spotting may partly result from inter-site mobility, preventing divergence in spot patterns between sites. In addition, colonisation history and continuously changing patterns of habitat availability in North Wales may limit temporal and spatial isolation of populations of *M. jurtina*. Differences in size are most likely related to environmental effects during larval development.

Résumé

Les auteurs ont mesuré les ocelles du dessous des ailes postérieures et l'envergure du Satyride «Le Myrtil», *Maniola jurtina* (L.), dans des séries récoltées dans le nord du Pays de galles, à 10 endroits dont on savait que leurs différences de climat, de géologie et d'habitat étaient à l'origine d'une diversité significative chez un autre Satyride, «L'Agreste», *Hipparchia semele* (L.). Chez les *Maniola jurtina* de tous ces endroits, les ocelles des deux sexes avaient la même forme, mais les envergures présentaient des différences significatives. Ces résultats ne concordent pas avec les règles qui établissent une relation entre le dessin des ocelles des ailes postérieures et le temps ou des différences d'activité et de sélection selon l'habitat. Les données sur les mouvements du Myrtil observés dans une autre station — Brereton Heath,

Cheshire — sont présentées pour suggérer que l'uniformité des ocelles constatée pourrait être en partie le résultat de la mobilité des Myrtils entre les localités : elle préviendrait la divergence dans l'aspect des ocelles selon l'habitat. Par ailleurs, la colonisation et les changements continus des types d'habitat disponibles dans le nord du Pays de Galles pourraient réduire l'isolation des populations de *M. jurtina* dans l'espace et dans le temps. Quant aux différences de taille, elles sont le plus vraisemblablement dues aux influences de l'environnement pendant le développement de la chenille.

Zusammenfassung

Untersucht wurden das Fleckenmuster der Hinterflügel-Unterseiten und die Flügelspannweite des Ochsenauges *Maniola jurtina*. Das Material stammte von 10 Fundorten in Nordwales, die sich in Klima, Geologie und Habitatstruktur unterscheiden. Letzteres führt bei einer anderen Satyrine, nämlich *Hipparchia semele*, zu einer signifikanten Diversität. Bei beiden Geschlechtern von *Maniola jurtina* war das Flügelmuster an allen Fundorten gleichförmig, die Größe dagegen signifikant unterschiedlich. Diese Ergebnisse stehen im Widerspruch zu Modellen, die das Hinterflügel-Muster mit dem Wetter oder mit habitatbedingten Aktivitätsunterschieden und Selektion korrelieren. Unter Berücksichtigung von Daten über Lokomotionsaktivitäten von einem anderen Fundort (Brereton Heath, Cheshire) wird vorgeschlagen, daß die beobachtete Gleichförmigkeit des Fleckenmusters teilweise daraus resultiert, daß zwischen den einzelnen Fundorten ein Individuenaustausch stattfindet. Dies verhindert Unterschiede im Fleckenmuster zwischen den Fundorten. Außerdem begrenzen die Besiedlungsgeschichte und das sich ständig verändernde Angebot an Habitaten in Nordwales die zeitliche und räumliche Trennung der Populationen von *M. jurtina*. Größenunterschiede sind höchstwahrscheinlich durch Umgebungseinflüsse während der Larvalphase bedingt.

Introduction

Populations of the meadow brown *Maniola jurtina* (L.) (Lepidoptera, Satyrinae) may differ in marginal hindwing spotting, size, emergence time and emergence period (Brakefield, 1984 ; Brakefield & Shreeve, 1992 ; Dennis, 1977). Such differences are not universal, with geographic patterns of uniformity being recognised throughout the geographic range of this butterfly (Dowdeswell & McWhirter 1967 ; Owen & Smith, 1993). Morphological differences which occur are described as the product of current selection associated with habitat structure and climate (Brakefield, 1984 ; 1987) or result from past events associated with changes in distribution and range during Pleistocene polyglaciation (Dennis, 1977 ; Shreeve, 1989). Differences of peak emergence times have been related to temperature experienced during development (Brakefield, 1987) whilst the duration of the emergence period has been

related to environmental heterogeneity and local adaptation of populations derived from a single ancestral population (Brakefield, 1987 ; Thomson, 1971 ; Dennis, 1971) or from more than one ancestral population (Dennis, 1977 ; Shreeve, 1989).

Within any population of *Maniola jurtina* there may be seasonal changes of morphological characters. Typically there are decreases of mean spot number, of the proportion of individuals with costally positioned spots and of wing expanse during the flight season (Creed, *et al.*, 1962 ; Brakefield, 1984 ; 1987). Such changes, which are not universal (e.g. Shreeve, 1989), are linked to differential development rates and pleiotropic effects.

Inter-population variation of marginal hindwing spotting in *Maniola jurtina* has been related to temperature, activity and predator evasion (Brakefield, 1984). It is argued that hindwing spots are emphasised in warm habitats since they can fully function as deflective characters in secondary defence when individuals are capable of effective escape flights. In cool habitats emphasis is placed on reduced spotting and crypsis since hindwing spots cannot act deflectively if low temperatures preclude flight activity and therefore escape. The model of Brakefield also relates spotting to habitat heterogeneity and to differences between male and female activity. Hindwing spotting is reduced and more uniform in populations of homogeneous habitats than those of heterogeneous habitats because fewer spot patterns will be successful in the former. In any habitat males will be more prominently spotted than females since emphasis is on deflection in males as they engage in more flight activity and on crypsis in the less active female.

Since hindwing spotting is heritable (Brakefield & van Noordwijk, 1985), variation between populations within any geographic area will be related to differences in selection pressures between populations and gene flow between these populations. In this paper we examine hindwing spotting and size of *Maniola jurtina* from a variety of sites in North Wales. Observations on *Hipparchia semele* (L.) (Lepidoptera, Satyrinae) at these sites have disclosed marked significant variation between populations. Individuals of both sexes from the Great Orme's Head are significantly dwarfed, have fewer and smaller wing spots and emerge earlier than butterflies from other sites. Individuals from sand dune habitats are significantly larger in wing expanse and have greater wing spotting than those from other lithologies, with the exception of those from dune populations adjacent to the Great Orme's Head, which apparently have been influenced by gene flow from populations on the Great Orme's Head (Dennis, 1972 ; 1977 ; unpubl. data). There

is therefore the expectation that *Maniola jurtina* from the same or similar sites will show interpopulation variation in response to similar environmental factors.

Materials and methods

To compare spotting and wing expanse of populations from different areas, samples of adults were collected during the peak flight period from 10 different sites in north Wales (Figure 1 and Table 1), many of which demonstrate heterogeneity in *Hipparchia semele*. For most sites samples of adults were collected over several days during the peak flight periods (mid-July) of the years 1969-1972. Individuals from Aberffraw were collected in mid-August 1972. Hindwing spots were recorded using x10 or x30 magnification and wing expanse was recorded as mid-thorax to forewing-tip length to 0.5 mm. using a scale rule. Spot number rather than spot area was measured because the former provides a simpler measure of the total spot area and spot number and position have been used to characterise populations in previous studies (see Brakefield, 1984).

Habitat heterogeneity was recorded by summing the number of different types of vegetation structures within the areas used by *Maniola jurtina*. Climatic data for the sample sites were not obtained directly but April-June mean temperature and July-September mean temperature and daily hours of sunshine are calculated for each site using the formulae given by White & Smith (1982). The first climatic variable



Fig. 1. The location of sample sites for *Maniola jurtina* in North Wales.

Table 1

The location, characteristics and sampling dates for collections of *Maniola jurtina* in North Wales

Site	N.G. Ref.	Altitude (m)	Aspect	Habitat	Habitat heterogeneity	Sampling dates
Great Orme	SH7683	0-100	Southwest facing slope	Limestone : grassland and scree	2	17/7/69 2-17/7/70
Little Orme	SH8282	0-100	Gentle slopes of all aspects	Limestone : grassland	3	22/7/69 9,26/7/70 1/8/72
Gloddaeth	SH8080	< 50	Southeast gentle slope	Limestone : tall grassland and woodland edge	4	25,26/7/70 1-24/7/70
Pydew	SH8179	100	North facing slope	Limestone : short grassland and woodland edge	3-4	15/7/70 5,18,21,23/7/70
Deganwy	SH7779	0-100	East facing slope	Volcanics : scrub	2	11,19/7/70 25/7/72
Colwyn Bay	SH8477	200	Gentle slopes of all aspects	Till over non-calcareous sediments : scrub and tall grassland	2	10,18/7/70 25/7/72
Conway Morfa	SH7779	< 50	Gentle slopes of all aspects	Sand : coastal grassland	2-3	18,25/7/72
Dulas Valley	SH9176	50-100	Mainly westerly aspect	Limestone : mixed grassland and woodland edge	2-3	2/8/70 17,25/7/72
Dolgarrog	SH7766	< 50	Gentle east facing slope	Peat & alluvium : woodland edge and acid grassland	3-4	20/7/72 1-7/8/72
Aberffraw	SH3568	< 50	Gentle slopes of all aspect	Sand : coastal dunes	2	13/8/82

Habitat heterogeneity is defined as the number of different types of habitats used by *Maniola jurtina*.

has a major influence on the timing of emergence (Brakefield, 1987), the others on the activity of adults during the flight season.

Intra- and inter-habitat movement data were collected, using mark-release recapture (MRR) techniques, during the period June 30 to July 29 1987, at Brereton Heath Country Park, Holmes Chapel, Cheshire. Intensive data on mobility could not be collected in North Wales because of the distances between the sites and also because development has eliminated some of the sites since the original samples were collected. At the Cheshire site individuals were sampled along a fixed transect route which covered the entire area, including 14 habitat zones and areas unsuitable for the butterfly. Habitats (Figure 2) could be clearly identified from demarcations in vegetation structure and the location of egg-laying and mating individuals. Population estimates were made using the method of Jolly (Begon, 1979).

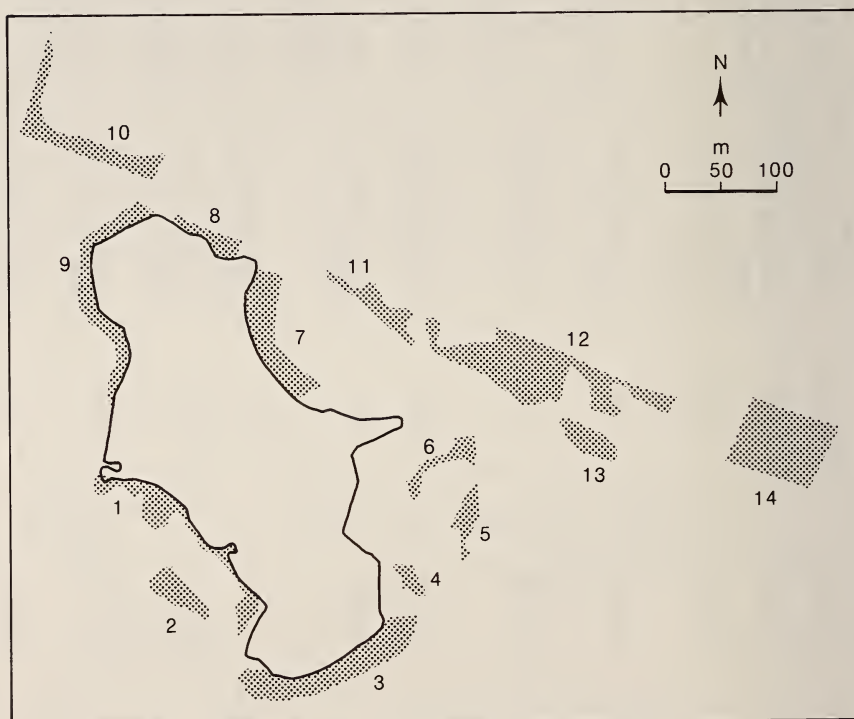


Fig. 2. The location of fourteen population units of *Maniola jurtina* at Brereton Heath, Cheshire.

Geographic patterns of spotting and size

For both sexes, spot pattern, spot combinations, mean spot number and costality indices are shown in Table 2a and 2b (see Brakefield & Shreeve, 1992 for spot pattern notation). There are no significant differences between samples from different sites in the total number of hindwing spots (males, $\chi^2_{(9)} = 11.04$, $P > 0.2$; females, $\chi^2_{(18)} = 20.53$, $P > 0.3$), nor for individual wing spots (spot 1 : males, $\chi^2_{(9)} = 12.77$, $P > 0.1$; females, $\chi^2_{(8)} = 8.09$, $P > 0.3$; spot 2 : females, $\chi^2_{(9)} = 7.41$, $P > 0.5$; spot 5 : females, $\chi^2_{(9)} = 12.45$, $P > 0.1$; spot 6 : males, $\chi^2_{(9)} = 10.85$, $P > 0.3$; females, $\chi^2_{(9)} = 12.45$, $P > 0.1$; other spots were either almost universally present or absent). For all sites, male spot number is unimodal at 2 spots and the commonest phenotype is splay 2; and in females, spot number is unimodal at 0 spots, the commonest phenotype being spot absence.

Sixty-four spot combinations are theoretically possible from the six hindwing spot locations; 15 were identified in North Wales and most were infrequent (Table 2a and 2b). Comparisons between sites for spot combinations (males, 010010 versus remainder, $\chi^2_{(9)} = 14.25$, $P > 0.1$; females, 000000 and 010000 versus remainder, $\chi^2_{(18)} = 23.66$, $P > 0.1$) also indicate homogeneity, as did a comparison between sites for costal-anal bias in spotting (individuals were scored as to sign, spots being registered as positive if costal, neutral if medial and negative if anal; males, $\chi^2_{(9)} = 5.04$, $P > 0.8$; females, $\chi^2_{(9)} = 12.54$, $P > 0.1$). Multivariate analyses of sites for frequencies of spot combinations revealed no conformity for sex, geographic location, habitat type or climate, contrasting with observations of *Hipparchia semele* (see Dennis, 1972, 1977).

Mean wing expanse of males and females is shown in Table 3. For both sexes there are differences of mean wing expanse between sites (males, $F_{(9,188)} = 5.38$; females, $F_{(9,190)} = 4.65$; $P < 0.001$ in both cases). The largest individuals are from Gloddeath and the smallest from Aberffraw. Mean size is not correlated with mean spot number in either sex (males, $r_s = 0.12$, females $r_s = 0.261$, N.S. in both cases). With the exception of female costality, mean spot number, costality and size of both sexes are not correlated with temperature (April-June) during the relevant developmental period, or temperature and sunshine hours during the flight period (July-September). Female costality is correlated with mean July-September daily hours of sunshine ($r_s = 0.79$, $P < 0.01$).

Table 2
Spot characteristics of a) male and b) female *Maniola jurtina* from ten sites in North Wales

a) males		Spot pattern															Mean spot number	Sample size
Site	000000	100000	010000	000010	110000	010010	000110	000011	110010	010110	010011	110110	110011	010111	110111	Costality		
Great Orme	1	0	0	6	0	37	0	0	8	1	5	0	2	0	2	47.0	62	
Little Orme	0	0	0	1	0	19	0	0	1	1	3	0	2	1	0	46.1	28	
Gloddath	0	0	0	4	0	13	0	0	5	2	4	1	5	1	1	46.1	36	
Pydew	0	0	0	3	0	30	0	0	4	2	4	1	1	0	0	48.0	45	
Deganwy	2	0	0	0	0	18	0	0	0	2	2	0	4	2	1	44.4	31	
Colwyn Bay	0	0	2	3	0	38	0	0	5	1	7	0	2	2	0	47.8	60	
Conway Morfa	0	0	0	1	0	26	0	0	8	0	3	1	3	1	0	51.9	43	
Dulas Valley	0	0	1	5	0	47	0	1	8	2	7	2	1	0	1	47.9	75	
Dolgarrog	0	0	1	8	0	56	0	0	11	3	10	1	5	1	3	46.7	99	
Aberffraw	0	0	0	0	0	12	0	0	2	2	1	0	1	1	3	42.3	22	
b) females		Spot pattern															Mean spot number	Sample size
Site	000000	100000	010000	000010	110000	010010	000110	000011	110010	010110	010011	110110	110011	010111	110111	Costality		
Great Orme	23	0	14	2	3	7	0	0	2	0	0	0	0	0	0	73.8	51	
Little Orme	13	0	6	4	0	2	0	0	1	0	0	0	0	0	0	58.8	26	
Gloddath	20	0	7	1	3	0	0	0	3	0	2	1	1	0	0	69.4	38	
Pydew	11	1	4	2	1	4	0	0	2	1	1	1	0	0	0	61.3	28	
Deganwy	12	0	7	1	3	6	0	0	4	0	0	0	0	1	0	68.3	34	
Colwyn Bay	19	0	5	4	2	11	0	0	2	0	1	0	1	0	1	56.3	46	
Conway Morfa	11	0	7	3	1	3	0	0	4	0	0	1	0	0	0	64.9	30	
Dulas Valley	18	0	10	5	1	4	0	0	5	0	0	0	0	0	0	65.0	33	
Dolgarrog	12	0	15	2	5	4	1	1	3	0	0	0	0	0	0	74.5	43	
Aberffraw	13	0	7	1	2	3	0	0	1	0	0	0	0	0	0	76.2	27	

Spot pattern combinations are given in a linear sequence for 6 spots placed costally to anally in a median band on the underside of the hindwing. Costality index is the percent of the two most costally placed spots to the sum of the number of the four costal and anal spots.

Table 3

Mean wingspan of males and females of *Maniola jurtina* from ten sites in North Wales

Site	Mean Wingspan (mm) ± s.e.	
	Male	Female
Great Orme	24.9 ± 0.23	26.4 ± 0.31
Little Orme	24.5 ± 0.20	26.3 ± 0.20
Gloddaeth	25.4 ± 0.32	27.5 ± 0.28
Pydew	24.4 ± 0.25	26.1 ± 0.25
Deganwy	25.1 ± 0.18	27.2 ± 0.18
Colwyn Bay	24.5 ± 0.21	26.6 ± 0.20
Conway Morfa	24.3 ± 0.21	26.0 ± 0.21
Dulas Valley	24.4 ± 0.18	26.5 ± 0.35
Dolgarrog	24.9 ± 0.19	27.1 ± 0.24
Aberffraw	23.6 ± 0.18	25.8 ± 0.28

Sample size = 20 in all cases except for males from Gloddaeth where N = 18

Mobility

The distribution of habitats on Brereton Heath is shown in Figure 2. The total population size rose to a peak of 163 males on July 12 and 161 females on July 22. Mean residence time for males is 9.7d and for females 7.2d. Some 24.7 per cent (118 of 761) of movements were between the 14 habitat patches ; this together with the pattern of cross movements (Figure 3) indicates that individuals on the heath belong to a single population. The pairwise frequency of cross-movements can be closely matched by an orthodox gravity model ($r_s = 0.69$, $P < 0.001$) :

$$M_{ij} = \frac{P_{ij}}{D_{ij}}$$

Equation 1

where M is the expected interactions, P is population size, and D is the direct distance between the populations ; the number of unique captures per habitat unit is used as a surrogate for population size. Habitat areas differ substantially in size, isolation, relative population size and density (Table 4), factors which can influence the ratio of between to within habitat movements. Out-movements, as a fraction of within habitat movement, are much greater from the ten small populations than from the four largest habitats ($r_s = 0.67$, $P < 0.01$). Out-movements also correlate negatively with population size ($r_s = -0.83$, $P < 0.001$), population density ($r_s = -0.70$, $P < 0.01$) and habitat area ($r_s = -0.65$, $P < 0.01$).

Movements into habitats can be modelled as part of the gravity equation ($r_s = 0.62$, $P < 0.05$) :

$$I_i = \sum_{j=1(j \neq i)}^{j=N} \frac{P_j}{D_j} \quad \text{Equation 2}$$

where I is the index of input into an area. A better predictor of in-movements is population size ($r_s = 0.94$, $P < 0.01$), but this relationship is influenced by the correlation of habitat size with the geographic parameters of neighbours in Equation 2. At Brereton Heath large habitats tend to be nearest to other large habitats ($r_s = 0.53$, $P < 0.05$), but there may also be a tendency for immigrants into larger more densely populated habitats to stay longer than those in sparsely populated habitats, and thus have a higher probability of being recorded during transect MRR events.

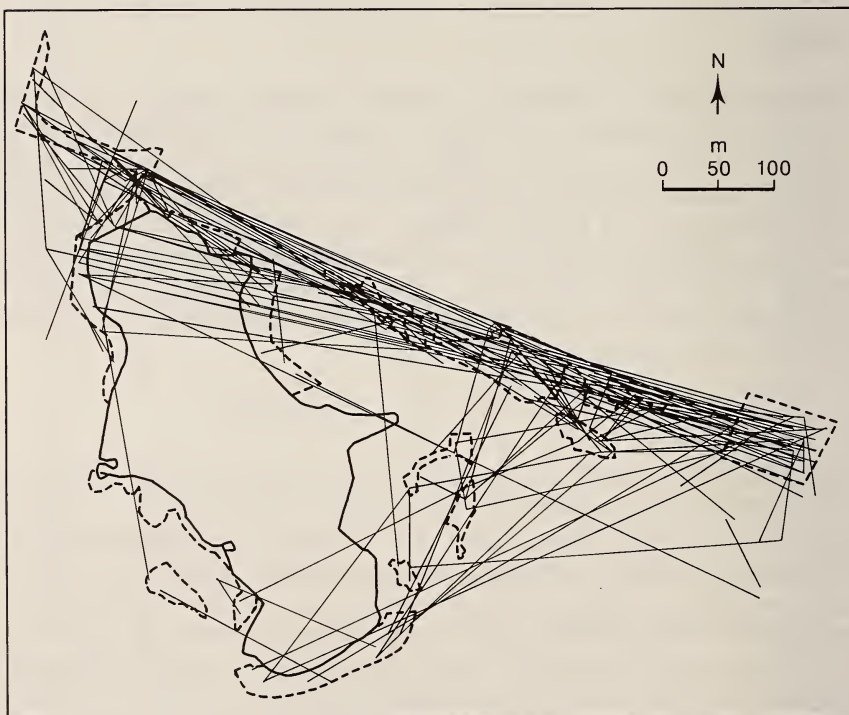


Fig. 3. Combined recorded movements of males and females between population units at Brereton Heath, Cheshire.

Table 4

Population and movement parameters, area and isolation of habitat units for the *Maniola jurtina* metapopulation on Brereton Heath, Cheshire

Habitat unit	Habitat area (x10m ²)	Mean isolation ¹ (m)	Nearest neighbour (m)	Population size ²	Population density	Number of movements out	Number of movements within	Number of movements to
1	19	186.7	24.3	3	0.16	1	0	1
2	12	235.5	24.3	4	0.33	1	0	1
3	38	191.7	18.9	23	0.16	7	10	4
4	6	185.1	18.9	5	0.83	3	2	0
5	9	170.0	14.0	11	1.20	5	5	5
6	9	150.7	14.0	10	1.10	5	2	4
7	20	148.2	19.0	16	0.80	9	4	4
8	8	215.4	19.0	7	2.10	9	1	6
9	31	217.9	16.0	83	2.70	23	72	14
10	33	291.5	16.0	73	2.20	19	65	33
11	17	161.3	8.0	33	1.90	14	9	11
12	72	134.9	8.0	291	4.00	43	248	51
13	10	215.8	14.0	24	2.40	12	4	10
14	56	334.0	59.0	187	3.30	23	151	26

1. Mean of minimum linear distances to other habitat units

2. The number of uniquely marked individuals

Movements of the butterfly on Brereton Heath indicate that it is capable of flying considerable distances in a short period of time and of crossing a range of obstacles including mown grass, open water and woodland. Only 2.8 per cent (39 of 1392) of all captures and only 3.6 per cent (27 of 761) of captures involving recorded movements were of ex-habitat individuals. When compared to the number engaged in cross-movements between habitats (24.7 per cent), this demonstrates that movements between habitats must be rapid. Recorded distances moved by the butterfly will depend on study area dimensions and for how long individuals can be traced or followed. The mean maximum range of individuals at Brereton Heath for those captured at least three times is for males $158.2 \pm \text{SE } 12.7 \text{ m}$ ($n = 130$) and for females $118.3 \pm \text{SE } 14.4 \text{ m}$ ($n = 66$). Some 25.5 per cent of individuals (50 of 196) recorded linear ranges greater than the mean distance between habitats (204 m) and 4.6 per cent greater than the furthest neighbour distance (429 m). 96.4 per cent achieved linear transfers greater than the mean nearest neighbour distance (19 m).

Discussion

Models of spotting in *Maniola jurtina* (Brakefield, 1984) and in other Satyrine butterflies, e.g. *Coenonympha tullia* (Dennis, Porter & Williams, 1986), lead to expectations of spot pattern differences between populations from sites in North Wales which differ in climate, lithology and habitat structure. No differences were detected. The distinctive patterns of morphological variation in *Hipparchia semele* (Dennis, 1972, 1977) were not repeated in *Maniola jurtina*. It is unlikely that this lack of variation is simply a result of the sampling methodology. If the samples came from populations with true spotting differences then confounding effects may result from sampling times and unknown seasonal changes of spot number within populations. If mean spot number declines with season then there is an expected negative correlation of spot number with temperature experienced during development and if mean spot number increases with season there is an expected positive correlation. No such correlations were found. Non-significant correlations of spotting attributes with any climatic variables can be most easily explained by proposing that there are no differences in the overall spotting patterns of the sampled populations. Wing expanse differs between sites but there are no consistent trends that can be related to site characteristics, as in the case of *Hipparchia semele*, although the relatively late time of sampling may account for the small size of individuals from Aberffraw.

We think that there are interesting implications within these data. Wing spotting, but not size, is consistent over a wide range of habitat types. Three possible explanations can be given. The first is that selection for spotting is the same in all habitats. The second is that these spots are neutral in their effect. The third hypothesis is that individuals of *Maniola jurtina* are sufficiently mobile to prevent stabilisation of alternative spot patterns in different habitat patches. With the present data none of these three hypotheses can be rejected. However, the first is unlikely because the differences between the sites are sufficiently large to expect differences of flight activity and requirements for the expression of secondary defence mechanisms. The second hypothesis may also be unlikely because predator attacks are directed at hindwing spot positions in samples of *Maniola jurtina* from other areas (Bengtson, 1981; but see Shreeve, 1989). Although data on mobility presented here is from a different area to North Wales the observed patterns of mobility demonstrate that the butterfly has a substantial capacity to move between habitat areas. Observations from Brereton Heath provide results intermediate between those of previous studies that have primarily considered intra-habitat (Brakefield, 1982) and inter-habitat movements (Baker, 1984). They contradict observations by Ford (1975) for movements between habitats on the Isles of Scilly and confirm those of Baker (1984) that the butterfly is a highly mobile species. Movements within the pattern of habitat patches at Brereton Heath suggest that the contraction and isolation of habitats, as has been occurring in North Wales, may encourage migration (*sensu* Baker, 1978) rather than lead to its reduction. Ground unsuitable for the reproduction and maintenance of the butterfly (i.e. mown grass, dense woodland, open water, urban structures) are not obstacles to movement. Correlations between habitat area, population size and density, out-movements and in-movements indicate that the greatest determinant of when to stay as opposed to when to leave is the presence of other individuals. Larger denser populations encourage individuals to stay within habitats. Nevertheless, there is a continual leakage of individuals from the largest populations which may be expected to generate diversity for dispersal genes.

Additional, circumstantial evidence for vagility in *M. jurtina* is provided by analysis of allozyme variation in south-east England (Goulson, 1993a; 1993b). Low mean F_{ST} values (0.015 – 0.023) point to little divergence between geographically separated locations and are consistent with values for other highly vagile insects whose populations are effectively panmictic.

Variation in size of individuals between the different sample sites cannot be explained by conventional models. Spot size and number are usually related to wing size, large individuals tend to have more and larger spots (Brakefield, 1984). Surprisingly there is no correlation between size and spot number for the North Wales samples. An explanation is that for the sampled populations immediate environmental effects (which may not be shown in averaged climatic data) contribute more to size variation than do any other effects. The absence of variation in size to match the disruptive geographic pattern in *Hipparchia semele* probably relates to the different habitats occupied by the two species and differences in their colonisation history within North Wales. *Maniola jurtina* does not frequent the scree slopes occupied by *H. semele* and would not have colonised the present habitats until forest clearance (< 5ka B.P.). Unlike *H. semele* it would not have a history of isolation on the Great Orme extending back to c. 9ka B.P. (Dennis, 1992). As habitats for *H. semele* are relatively stable compared to those of *M. jurtina*, which is dependent on changing patterns of cultivation and grazing, *M. jurtina* populations probably share a more recent colonisation history and probably have a history of repeated local extinction and recolonisation, the latter aided by their mobility.

In conclusion, the results presented here demonstrate homogeneity of spot pattern between sites despite climatic and structural differences between sites. Spotting is similar to that over much of the range of the species. North Wales populations are similar to others and correspond to the general southern and central spot stabilisation of Britain (Dowdeswell & McWhirter, 1967 ; Dowdeswell, 1981). We suggest that in North Wales at least, inter-site mobility may largely preclude differentiation in climatically dissimilar sites and that differentiation of *Maniola jurtina* observed elsewhere will only occur when populations have been effectively isolated. Instability in habitats, shifting locations and recent colonisation history in North Wales have thwarted the evolution of size and hindwing spot pattern variation in *Maniola jurtina*. Differences between sites in adult size, are, we suggest, the result of the interaction of developmental rate and site temperature ; warm sites promote development and allocation of resources to body mass.

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Autor(en)/Author(s): Shreeve Timothy, Dennis Roger L.H., Williams W. Robert

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