

## Spot distribution in *Maniola jurtina* (Linnaeus, 1758) (Lepidoptera : Nymphalidae, Satyrinae) in Central Spain

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### Summary

The pattern of wing spotting in the satyrine *Maniola jurtina* (Linnaeus, 1758) was investigated in a sample of over 900 collection specimens from Central Spain. The frequency distributions of spots, and their relationships with other variables (date of collection, adult size, site elevation), were determined and compared with published data concerning Northern and Southern Iberian populations.

The general spotting pattern fits well to those described from South Iberian populations (especially from the Portuguese Algarve), showing no transition towards North Iberian phenotypes. The number of spots decreases towards the end of the summer season, a trend that is shared by Mediterranean populations that are phenotypically distant (e.g., Iberian and Italian). This may be taken as evidence for a relationship between female aestivation behaviour and some kind of selection against high-spotted morphs. However, the fact that the same trend appeared in both sexes (while males are not known to aestivate) indicates that other underlying factors probably exist, and that these may operate on both sexes. This idea is reinforced by the fact that spotting was significantly correlated to adult size.

### Resumo

O padrão de pontos existentes nas asas de *Maniola jurtina* (Linnaeus, 1758) foi observado numa amostra com mais de 900 espécimes pertencentes a coleções entomológicas, recolhidos na zona Central de Espanha. Analisou-se a distribuição de frequências dos pontos, a relação com outras variáveis quantificadas (tamanho dos indivíduos, data e altitude) e procedeu-se à comparação destes dados com outros trabalhos publicados sobre populações da Península Ibérica.

A distribuição de pontos é semelhante ao descrito para populações do Sul (especialmente à zona do Algarve, Portugal). As populações do Sul e Centro da Península Ibérica são homogéneas quanto a esta característica, não tendo

sido detectada uma zona de transição fenotípica ou a fronteira com o Norte da Península Ibérica.

Verificou-se a diminuição do número de pontos ao longo do Verão, particularmente nas fêmeas. É um fenómeno que ocorre igualmente noutras populações mediterrâneas e que é independente da distribuição dos pontos. Tem sido explicado pela acção da selecção natural, que elimina os fenótipos com maior número de pontos, associada a um comportamento de estivação das fêmeas. No entanto, o facto de também ocorrer diminuição nos machos (que não estavam) e existir uma correlação significativa entre o padrão de pontos e o tamanho dos adultos, parece indicar que existem outros factores que actuam em ambos os sexos.

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## Introduction

The distribution of spots on the underside of the wings of the meadow brown butterfly, *Maniola jurtina* (Linnaeus, 1758), has been the subject of numerous studies over more than 40 years. Dowdeswell and McWhirter (1967) analysed samples from the whole geographic range of the species in order to evaluate the variability of this feature. They found a highly uniform spotting pattern over most of continental Europe and Great Britain which they termed "General European Area". In addition, smaller zones ("peripheric areas") showed particular spotting patterns. It seems that the spot distribution is stable over long periods of time, as well as over wide geographic areas, in the two sexes (Dowdeswell & McWhirter, 1967 ; Ford, 1975 ; Brakefield, 1984 ; Brockie, 1972 ; Shreeve, Dennis & Williams, 1996). In general, the females display a remarkably constant spotting pattern while the males, although unimodal at 2 spots, are far more variable (Ford, 1975). The General European Area was explained as a result of the powerful action of natural selection, which would produce a uniform pattern in spite of important environmental variation. Because of their small size and isolated character, the peripheric areas might have achieved different patterns by adjustment to local conditions (Brockie, 1972). Field data indicate that intra-seasonal shifts in spot distribution are restricted to these peripheric areas. While natural selection is generally accepted as the ultimate cause of these patterns, there is no agreement about the precise factors that are responsible for such variation. Proposed explanations have invoked climate (e.g. by Bengtson, 1978 ; Scali, 1972), behavioural adaptation (Brakefield, 1984), habitat heterogeneity (McWhirter, 1957) and predation (Brakefield, 1984 ; Owen & Smith, 1990).

The situation on the Iberian Peninsula (one of the peripheric areas) is not well studied. There is some evidence indicating sharp differences

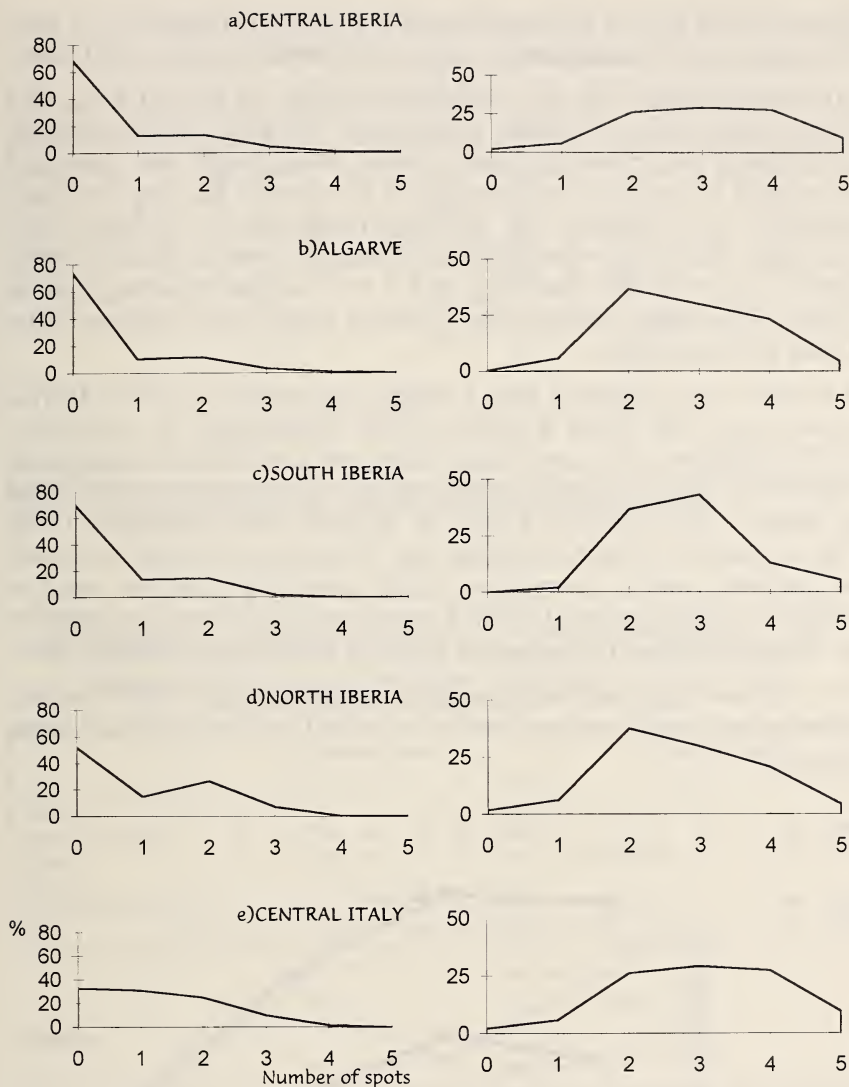
between the Northern and the Southern Iberian populations, the latter being characterized by a very low spot average in females (large modes at 0 spots) and a high spot average in males (mode at 2-3 spots), as well as by particular costality values, high in females and low in males (see Owen & Smith, 1993). The work made on South European populations (Italy : Scali & Masetti, 1975 ; Algarve : Owen & Smith, 1993) revealed that a marked decrease in female spotting occurs along the summer (*i.e.*, intra-seasonal shift). Since the long summer drought has important effects on the behaviour and phenology of the species in its Mediterranean range (Masetti & Scali, 1972 ; García-Barros, 1987), it is likely that some of the peculiarities of the South European peninsular populations could be related to climatic factors, and more specifically to the presence of a long, hot and dry summer season.

The present work relies on data gathered from populations in the central area of the Iberian Peninsula, which are presumably adapted to a long, adverse summer (García-Barros, 1987). On this basis, the aims of this study are : First, to make available updated data from Central Spain, in order to contribute to the delimitation of the boundary between the North and South spotting pattern of the species within Iberia. Second, and related to the former, to check whether or not the spotting pattern of Central Spanish *M. jurtina* is consistent with that of South Iberian populations. Third, to assess the relationship between the presence of a dry summer period (and female aestivation behaviour) and spotting, by trying to discover whether a seasonal shift occurs in this area. Finally, to investigate the relationships between spotting and two variables (adult size, elevation) that might be related to spotting, and might help to explain part of the variation found as a result of phenotypic plasticity.

## Material and methods

The sample consisted of 925 set butterflies from the collections at the Universidad Autónoma de Madrid (661 specimens), Natural History Museum at Madrid (167), and the Universidad Complutense de Madrid (97). Collection dates cover a period of 80 years (1912 to 1991), and the selected area spreads over about 200 km around Madrid city, with individuals collected in the provinces of Madrid, Segovia, Guadalajara, Cuenca, Avila and Teruel. This area is characterized by an important elevational gradient (400 to 1500 m in our samples). To cope with this heterogeneity, we compared every result from the pooled sample with





LEFT: FEMALES; RIGHT: MALES

Fig. 1. Spot distribution in Southern populations (x-axis = number of spots ; y-axis = %).  
a) data from this study  
b) data from Owen & Smith (1993)  
c), d) data from Dowdeswell & McWhirter  
e) data from Scali & Masetti (1975)

those derived from a sub-sample (443 individuals) collected by A. Pino in a single site (Casa de Campo, close to the city of Madrid, 1980-1981).

All measurements and spot counts were made on the left wing, and by the same person, to ensure consistency. The spots on the underside of forewing and hindwing were counted. Wing length was measured from base to apex of the forewing, to the nearest 1.0 mm. For each specimen, the collection site elevation (meters a.s.l.) and date were recorded. The spots were labelled following Owen & Smith (1993), that is 1 to 5 on the hindwing, and 1 to 4 on the forewing (anal to costal). The Splay, Median and Costality index were calculated after Owen & Smith (1993).

The data were compared with available information on other Iberian areas (data after Owen & Smith, 1993 ; Dowdeswell & McWhirter, 1967). Published data from Italy, Wales and the Swedish Archipelago were included as a contrast (using the spot frequencies given by Scali & Masetti, 1975 ; Shreeve, Dennis & Williams, 1996 ; Bengtson, 1978). The frequencies of each hindwing spot in males and females were used as variables, and a correlation matrix generated. This was used to construct a dendrogram (UPGMA procedure, with Pearson correlation as distance estimate) showing the affinities between the different areas.

For regression and correlation analyses, wing length was logarithmically transformed, and spotting (number of spots) was squared-root transformed.

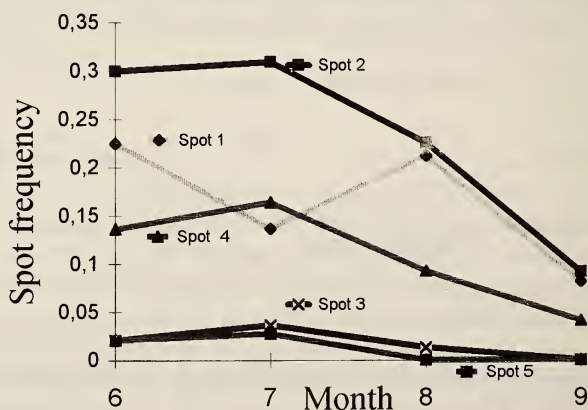


Fig. 2. Seasonal variation of spot average in the Central Iberian sample [bars :  $\pm$  standard deviation].

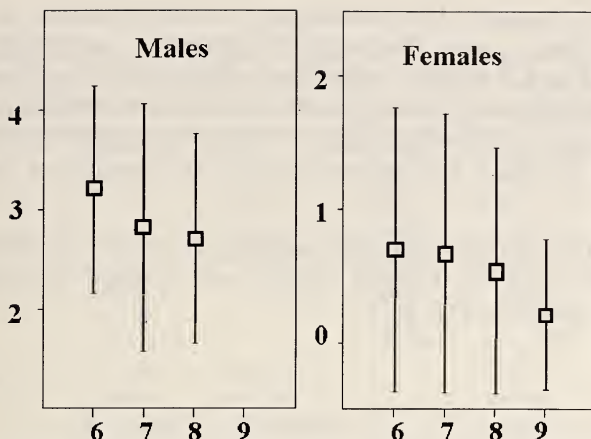


Fig. 3. Seasonal variation in the frequencies of individual spots (spot 1 = costal, to spot 5 = anal) in *Maniola jurtina* (Linnaeus, 1758) from Central Iberia.

Table 1

Number of spots on the hind- and forewing of *Maniola jurtina* (Linnaeus, 1758) from Central Spain (pooled sample), and a single site (Casa de Campo).

The figures given summarize the number of individuals with 0 to 5 spots, sample size (n), and mean number of spots (x)

	N° hindwing spots								N° forewing spots							
	0	1	2	3	4	5	n	x	0	1	2	3	4	n	x	
Males																
Casa de Campo	5	6	50	61	49	13	184	3.000	6	179	0	0	0	185	0.968	
Total	7	20	92	109	97	34	359	3.033	10	348	2	0	0	360	0.978	
Females																
Casa de Campo	161	35	32	13	1	1	243	0.605	0	188	51	8	1	248	1.282	
Total	390	72	76	26	5	2	571	0.581	0	442	118	19	2	581	1.279	

## Results

The frequencies of hindwing and forewing spot numbers are given in Table 1. Male and female spot distributions were markedly different in both forewing and hindwing patterns. Both sexes showed little variation in forewing spotting, which was particularly low in the males. Hindwing spot average was of 3.033 in males and 0.581 in females. A comparison of the spot distributions of the pooled sample and the collection from Casa de Campo presented no evidence for a statistically significant difference ( $X^2_{(5)} = 3.361$  ;  $P > 0.05$ , for males ;  $X^2_{(3)} = 0.747$  ;

$P > 0.05$ , for females). The females are strongly unimodal at 0 spots, while males have a more “flat-topped” distribution, with high proportions of 2, 3 and 4 spotted individuals (Fig. 1a). Table 2 shows the percentage of hindwing phenotypes in our sample, as well as the overall Costality, Splay and Median indices. Twenty-four different phenotypes were found, of which five are restricted to the female sex and six to the males.

The comparison between our data and those from other areas indicated close affinity between Central Spain and Algarve (the clustering hierarchy is shown in Fig. 4).

Table 2

Hindwing phenotypes found in female *Maniola jurtina* (Linnaeus, 1758) from Central Iberia, and their relative frequencies and values for three descriptive indices, that are often used in research on this species (see text)

Phenotypes	Males (%)	Females (%)
00000	1.9	68.3
10000	0	3.4
01000	0	6.1
00010	5.3	2.8
11000	0	9.1
10010	0	0.3
01010	22.3	3.2
00110	0.3	0
00011	2.8	0
11010	8.9	4.2
01110	1.7	0
01011	18.9	0.2
11110	1.9	0.5
11011	22.6	0.3
01111	2.5	0
11111	9.5	0.3
00100	0	0.2
10100	0	0.2
01100	0	0.3
00001	0.3	0.2
11001	0	0.2
01001	0.3	0
10011	0.8	0
10001	0	0.2
Total	359	571
Costality Index	0.457	0.799
Splay Index	0.56	0.187
Median Index	0.159	0.016

Table 3

Relationships between the number of spots, size, date of capture and elevation, as measured by Pearson correlation ( $n$  = sample size ;  $p$  = significance level) ; [females-upper right half of the table ; males- lower left half]

	Elevation	Date	Forewing length	N hindwing spots	N° forewing spots
Elevation		0.166 $n = 471$ $p = 0.0003$	- 0.0854 $n = 560$ $p = 0.0434$	0.0121 $n = 570$ $p = 0.7734$	0.0191 $n = 580$ $p = 0.6457$
Date	0.0612 $n = 280$ $p = 0.3072$		- 0.0496 $n = 450$ $p = 0.2940$	- 0.2096 $n = 460$ $p = 0.0000$	- 0.073 $n = 469$ $p = 0.1144$
Forewing length	- 0.1248 $n = 347$ $p = 0.0201$	0.0328 $n = 274$ $p = 0.5886$		0.1536 $n = 552$ $p = 0.0003$	- 0.0058 $n = 560$ $p = 0.8906$
N° hindwing spots	- 0.0151 $n = 355$ $p = 0.7775$	- 0.1868 $n = 281$ $p = 0.0017$	0.199 $n = 350$ $p = 0.002$		0.1627 $n = 571$ $p = 0.0001$
N° forewing spots	0.16 $n = 356$ $p = 0.7636$	0.0803 $n = 282$ $p = 0.1788$	0.0279 $n = 351$ $p = 0.602$	- 0.0128 $n = 359$ $p = 0.8093$	

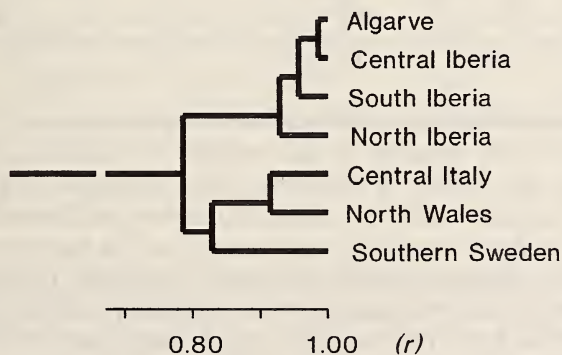


Fig. 4. Dendrogram showing the affinities between Central and other Iberian populations of *Maniola jurtina* (Linnaeus, 1758). Data from three non-Iberian populations are included as a contrast. Affinities are based on the frequencies of spots on the hindwings of females and males, using Pearson correlations as a measure of similarity and the unweighted arithmetic average clustering method (UPGMA). [Algarve = data from Owen & Smith (1993) ; North and South Iberian = Dowdeswell & McWhirter (1967) ; North Wales = Shreeve *et al.* (1996) ; Southern Sweden (island populations) = Bengtson (1978)].



The correlations between spot number, date of capture, wing size and collection site elevation are shown in Table 3. Results for both sexes were consistent, the number of hindwing spots being significantly correlated with date and forewing length. In other words, larger individuals tend to present a higher number of spots, while spotting decreases during the season (see also Fig. 2 and Table 4). Elevation was negatively correlated with forewing length in both sexes. Since variation in male forewing spotting was small, and female fore- and hindwing spotting were positively correlated (Table 3), all subsequent analyses were restricted to the number of hindwing spots.

Table 4  
Monthly variation in spotting patterns (hindwing underside)  
n = sample size ; x = mean values)

Month	N° hindwing spots						n	x
	0	1	2	3	4	5		
Males								
May	0	0	8	4	3	3	18	3.055
June	1	8	36	59	56	18	178	3.208
July	5	5	24	25	20	7	86	2.826
August	0	5	20	12	11	3	51	2.714
Females								
May	6	0	1	0	0	0	7	0.286
June	93	21	20	11	1	1	147	0.701
July	71	14	18	5	1	1	110	0.673
August	105	19	20	5	2	0	151	0.543
September	85	8	5	1	0	0	99	0.214

Stepwise multiple regression analyses were used to discover the relative importance of each variable in the number of hindwing spots, and to control for any effects of elevation (since elevation and date were correlated in females : Table 3). Several runs were performed regressing spot number on date, wing length and elevation. The last three variables were entered in different orders, and both separately for each sex or for all the data pooled. All analyses were consistent, and thus the results are not given in full. The variable „date” accounted for the largest proportion of the variance in spot numbers ( $R^2 = 0.033$  for males ;  $R^2 = 0.043$  for females). Adding the variable „forewing length” to the regression raised the explanatory power ( $R^2 = 0.064$  for males ;  $R^2 = 0.063$  for females) ; the effect of „elevation”, once the other two variables had been entered, was negligible ( $R^2 = 0.061$  for males ;  $R^2 = 0.062$  for females). We may thus conclude that date is the main source of variation related to spot number.

Fig. 2 represents monthly mean spot number. The trend towards low spotted patterns as the summer progresses is more evident in the females, and seems to operate in the same way for each of the individual spots (especially for spots 1, 2 and 4, since spots 3 and 5 are relatively rare ; see Fig. 3). Chi-square comparisons revealed significant differences between June and September females ( $X^2_{(3)} = 15.396$  ;  $0.001 < P < 0.01$ ), as well as between July and September females ( $X^2_{(3)} = 12.540$  ;  $0.001 < P < 0.01$ ). As far as our material allowed for more detailed comparisons, the results are generally true for the samples from Casa de Campo (see Table 5).

Table 5

Relationship between the number of hindwing spots and date and wing size, measured in butterflies from a single population (Casa de Campo, Madrid). Values are Pearson correlation coefficients (n = sample size ; P = significance level)

	n	Date	Wing length
Males			
1980	95	- 0.142 (P = 0.171)	- 0.013 (P = 0.09)
1981	79	- 0.392 (P < 0.001)	- 0.085 (P = 0.455)
1980/ 1981	174	- 0.250 (P < 0.001)	- 0.015 (P = 0.844)
Females			
1980	163	- 0.268 (P = 0.016)	0.016 (P = 0.016)
1981	63	- 0.294 (P = 0.02)	0.201 (P = 0.115)
1980/ 1981	226	- 0.273 (P < 0.001)	0.175 (P = 0.008)

## Discussion

The comparison between the spot distributions, as well as the Costality, Median and Splay index values, reveals high similarity between Central and South Iberian populations (e.g. data from Owen & Smith, 1993 and this study), especially in females. In agreement with previous studies, males are more variable than females (in fact, males might be used to characterize Central Iberian populations relative to e.g. those from Algarve). Our results show no South to North transition, and thus support the contention that most of the Iberian Peninsula is occupied by a stable phenotypic distribution, which probably coincides with the so-called subspecies *M. jurtina hispulla* (Esper, [1805]) (Thomson, 1973).

Whether or not a transition zone exists, not far away to the North, remains unknown.

Our finding of a seasonal trend towards reduction in spot number in females (and less markedly in males) fits the similar intra-seasonal shifts described from other Mediterranean areas, like Algarve (Owen & Smith, 1993) and Central Italy (Scali, 1975), where the females are known to aestivate (Scali & Masetti, 1975; Brakefield, 1979; García-Barros, 1987). This suggests a relationship between female aestivation and the seasonal change in spot frequencies. A selective elimination of the high-spotted phenotypes may account for this pattern and would explain the homogeneous, low-spotted, female phenotypes found in September (as formerly proposed, e.g. Scali, 1972). It is thus interesting that a similar trend was discovered in the males, because no evidence for male aestivation has been published. The negative correlation between spot number in males and date is not much lower than the one determined for the females. The male flight period is shorter than that of females (few are found in September), and this may contribute to obscure the relationship. On this basis, variables that may act in the two sexes — including seasonally determined phenotypic variation — might help in explaining seasonal spot variation in *M. jurtina*.

None of the quantitative variables tested in this study was highly correlated with the spot number, even when the correlations were statistically significant. This may be due, in part, to the heterogeneous condition of our sample, but also suggests an important amount of variation due to other factors. Assuming a relationship between aestivation and spot selection, some relationship between spotting and elevation might be expected (as observed in Italy, Scali & Masetti, 1975). The cooler mountain climate (and subsequently shorter aestivation period) should lead to higher spot frequencies. This is not supported by our data: elevation is correlated to adult size, but has no obvious relationship with spot patterns.

Intra-seasonal spotting shifts and the female aestivating behaviour seem to be generalized features of the Mediterranean area, independently of the spot distribution. If the relationship between these two factors can be demonstrated, the evidence would suggest either convergent phenological adaptation at the population level, or fast genetic divergence after the stabilization of a "Mediterranean adapted" population. Further studies on the behaviour and phenology of *Maniola jurtina* in this area would probably contribute to our understanding of the precise mechanisms related to spot selection.



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