

On the colour polymorphism of *Philaenus spumarius* (L.) (Homoptera, Cercopidae) in Portugal

J. A. Quartau & P. A. V. Borges

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On the colour polymorphism of Philaenus spumarius (L.) (Homoptera, Cercopidae) in Portugal.— A total of 7,967 specimens (4,354 males and 3,613 females) of the meadow spittlebug *Philaenus spumarius* (L.) collected in three different habitats at Fontanelas (Sintra) were analysed in terms of the colour morph frequencies. Eleven different morphs were encountered: *populi* (POP), *typicus* (TYP), *trilineatus* (TRI), *marginellus* (MAR), *lateralis* (LAT), *flavicollis* (FLA), *gibbus* (GIB), *ustulatus* (UST), *quadrimaculatus* (QUA), *albomaculatus* (ALB), and *leucophthalmus* (LOP). For males and in decreasing order of frequency the following morph groups and morphs proper were found: TYP group (95.38%), TRI group (3.70%), LCE group (0.85%), and LOP group (0.07%); and for females TYP group (88.79%), TRI group (4.01%), MAR (3.32%), LOP group (1.88%), LCE group (1.74%), and LAT (0.25%). As expected, the TYP group (POP + TYP) was more frequent in males than in females (about 95% vs. 89%, respectively). Moreover, most melanic morphs were exclusively (MAR, LAT, ALB, and LOP) or better represented (FLA and QUA) in females than in males. Results also show that there appear to be differences regarding females among the three habitats studied, in spite of being practically contiguous. The coolest of all three habitats (a *Pinus pinaster* woodland with a shrub community dominated mostly by *Ulex europaea*) showed the highest frequencies of the melanic morphs. It is therefore suggested that among other factors, thermal melanism plays an important selective role in the colour polymorphism of the meadow spittlebug at Fontanelas.

Key words: *Philaenus spumarius*, Colour polymorphism, Thermal selection, Portugal.

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J. A. Quartau, Centro de Biologia Ambiental, Depto. de Zoologia e Antropologia, Fac. de Ciências de Lisboa, C2, Campo Grande, 1700 Lisboa, Portugal. - P. A. V. Borges, Depto. de Ciências Agrárias, Universidade dos Açores, Terra Chã, 9702 Angra do Heroísmo Codex, Terceira, Açores, Portugal.

Introduction

The meadow spittlebug *Philaenus spumarius* (L.) is one of the commonest cercopids in the Palaearctic and other temperate regions, where it occurs in most terrestrial habitats, namely in meadows, waste ground and roadsides (STEWART & LEES, 1996). It is a highly polyphagous species with preference for nitrogen-fixing plants (WEAVER & KING, 1954; THOMPSON, 1994). It has been recorded as a pest of forage crops, strawberries and perennial herbs (e.g. OSBORN & KNILL, 1939; WEAVER & KING, 1954; HALKKA et al., 1967).

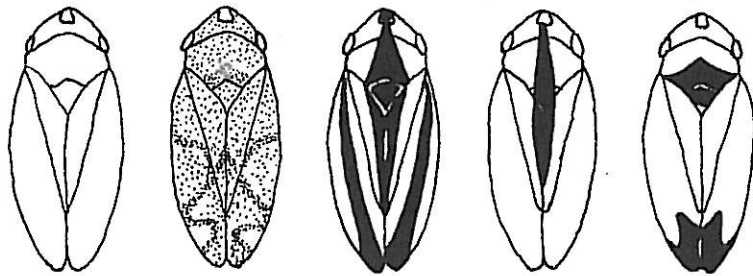
Besides being widespread in the Palaearctic region, the meadow spittlebug also became largely established in North America (THOMPSON & HALKKA, 1973; HAMILTON, 1979) and has recently colonized New Zealand (ARCHIBALD et al., 1979; THOMPSON, 1984b), Hawaii (ZIMMERMAN, 1948), and the Azores (LINDBERG, 1941; QUARTAU et al., 1992; SILVA & TAVARES, 1995). QUARTAU et al. (1992) found three morphs (TYP, POP and LOP) of the meadow spittlebug in low and high altitude grasslands in the largest of the Azorean Islands (S. Miguel) during field-work in 1979 and it should be corrected that it was LINDBERG (1941) who first reported the species for the Azores (S. Miguel) based on material collected by R. Frey. Very recently, intensive collecting has been carried out especially by the junior author in montane grasslands of three other Azorean Islands (S. Maria, Pico and Terceira), but so far the species seems to have colonized only the island of S. Miguel.

Throughout its range, populations of the meadow spittlebug show striking colour and pattern variation on both the dorsal and ventral body surfaces. Especially the dorsal polymorphism has been widely described and illustrated (e.g. HALKKA, 1962; LEES et al., 1983), there being generally recognized eleven most commonly occurring morphs under the control of seven allele at a single autosomal locus (HALKKA et al., 1973, 1975a). These colour phenotypes have been ascribed the following varietal names (fig. 1): POP. *populi*, TYP. *typicus*, TRI. *trilineatus*, MAR. *marginellus*, LAT. *lateralis*, FLA. *flavicollis*, GIB. *gibbus*, LCE. *leucocephalus*, QUA. *quadrimaculatus*, ALB. *albomaculatus*, and LOP. *leucophthalmus*. Some authors also refer to three additional morphs, namely, VIT. *vittatus*, PRA. *praeustus*, and UST. *ustulatus*, the two first often considered as minor modifications of TRI. *trilineatus*, and UST a very rare morph which seems to be a variant within the LOP complex (HALKKA, 1988). Of the eleven most common morphs, five are essentially pale with limited patterning (POP, TYP, TRI, VIT, and PRA) and the remainder (MAR, LAT, FLA, GIB, LCE, QUA, ALB, and LOP), which are dark with various combinations of pale markings on the elytra, head and prothorax, are generally considered melanic (STEWART & LEES, 1996).

The colour polymorphism is known to be of the balanced type (e.g. HALKKA et al., 1976; HALKKA & HALKKA, 1990), since there is temporal constancy of the allele frequencies with fluctuations of very small amplitude (e.g. HALKKA & MIKKOLA, 1977) and the return to polymorphic equilibrium following experimental perturbation (HALKKA et al., 1975b).

Fig. 1. The main colour morphs in *Philaenus spumarius*. Non-melanic phenotypes above the dashed line, melanics below. (For abbreviations see the text). Some morphs were grouped as follows: TYP group (POP + TYP), TRI group (TRI + VIT), LCE group (FLA + GIB + LCE), and LOP group (UST + QUA + ALB + LOP) (THOMPSON & HALKKA, 1973; STEWART & LEES, 1996).

Principales morfismos de color en Philaenus spumarius. Los fenotipos no melánicos por encima de la línea discontinua, los melánicos por debajo. (Para abreviaturas ver el texto). Algunos morfismos se han agrupado de la siguiente manera: grupo TYP (POP + TYP), grupo TRI (TRI + VIT), grupo LCE (FLA + GIB + LCE), y grupo LOP (UST + QUA + ALB + LOP) (THOMPSON & HALKKA, 1973; STEWART & LEES, 1996).



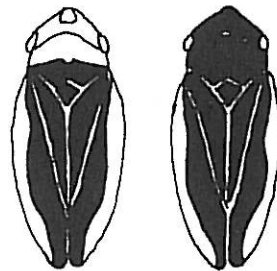
POP

TYP

TRI

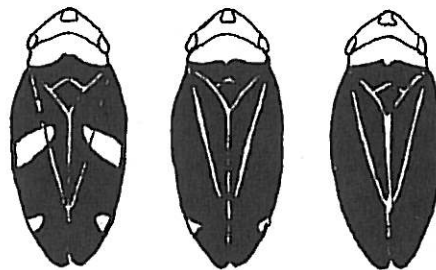
VIT

PRA



MAR

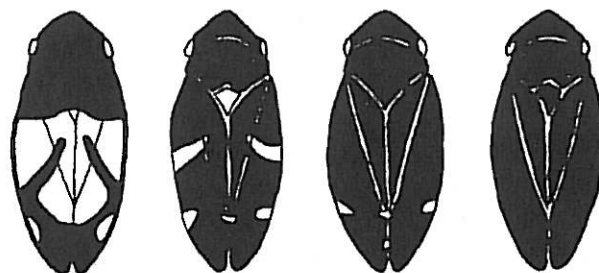
LAT



FLA

GIB

LCE



UST

QUA

ALB

LOP

Table 1. Colour morph numbers of *Philaenus spumarius* for both sexes (M. Males; F. Females) in the three habitats at Fontanelas (Sintra, Portugal) during 1988. (For abbreviations see the text.)

Cantidad de morfismos de color de Philaenus spumarius para ambos sexos (M. Machos; F. Hembras) en los tres hábitats de Fontanelas (Sintra, Portugal) durante 1988. (Para abreviaturas ver el texto.)

	Sex	Colour morphs											Total
		POP	TYP	TRI	MAR	LAT	FLA	GIB	UST	QUA	ALB	LOP	
Habitat A													
20 III	M	5	6	0	0	0	0	0	0	0	0	0	11
	F	0	9	0	0	0	2	0	0	2	1	0	14
30 III	M	58	83	10	0	0	0	0	0	0	0	0	151
	F	36	100	4	3	0	4	0	1	6	0	0	154
7 IV	M	59	117	4	0	0	3	0	0	0	0	0	183
	F	35	142	11	9	1	6	1	0	1	1	0	207
24 IV	M	140	267	13	0	0	4	0	0	0	0	0	424
	F	87	290	9	16	3	5	0	0	0	0	0	410
22 V	M	64	72	3	0	0	0	0	0	0	0	0	139
	F	38	53	5	5	1	0	0	0	3	0	1	106
Sub-total	M	326	545	30	0	0	7	0	0	0	0	0	908
	F	196	594	29	33	5	17	1	1	12	2	1	891
Habitat B													
24 IV	M	8	24	1	0	0	0	0	0	0	0	0	33
	F	5	22	1	2	0	1	0	0	1	0	0	32
22 V	M	19	54	1	0	0	0	0	0	0	0	0	74
	F	9	44	2	4	0	3	0	0	4	1	0	67
25 IX	M	10	16	0	0	0	0	0	0	0	0	0	26
	F	12	37	2	2	0	2	0	0	4	0	3	62
Sub-total	M	37	94	2	0	0	0	0	0	0	0	0	133
	F	26	103	5	8	0	6	0	0	9	1	3	161
Habitat C													
25 IV	M	331	497	43	0	0	12	1	1	2	0	0	887
	F	152	513	37	24	0	10	1	0	8	0	1	746
8 V	M	278	400	27	0	0	2	1	0	0	0	0	708
	F	171	286	22	17	2	5	0	0	8	0	0	511
29 V	M	320	399	26	0	0	6	0	0	0	0	0	751
	F	206	303	19	15	2	13	0	0	9	0	0	567

Tabla 1 (cont.)

	Sex	Colour morphs											Total	
		POP	TYP	TRI	MAR	LAT	FLA	GIB	UST	QUA	ALB	LOP		
19 VI	M	308	409	27	0	0	4	0	0	0	0	0	0	748
	F	163	341	24	20	0	7	0	0	7	0	1	563	
24 VII	M	64	98	6	0	0	3	1	0	0	0	0	172	
	F	38	70	7	3	0	2	0	0	3	0	0	123	
25 IX	M	14	33	0	0	0	0	0	0	0	0	0	47	
	F	16	30	2	0	0	1	0	0	2	0	0	51	
Sub-total	M	1,315	1,836	129	0	0	27	3	1	2	0	0	3,313	
	F	746	1,543	111	79	4	38	1	0	37	0	2	2,561	
Habitat A+B+C	M	1,678	2,475	161	0	0	34	3	1	2	0	0	4,354	
	F	968	2,240	145	120	9	61	2	1	58	3	6	3,613	

Melanic colour forms are striking to the eye, less common than their non-melanic counterparts, and occur at higher frequency among females or are even limited to this sex. This is the case of many Finnish populations where morphs MAR, LAT, GIB and LCE are entirely restricted to the females, but this generalization does not apply everywhere (STEWART & LEES, 1996). However, it can be generalized that the great majority of melanics are female. In Portugal very little attention has been given to the colour polymorphism of *Philaenus spumarius*. The meadow spittlebug was reported for Portugal last century (LETHIERRY, 1877) and was soon found to be quite widespread (e.g. SEABRA, 1930). Moreover, ten morphs were recognized as varieties (*populi*, *typicus*, *trilineatus*, *praeustus*, *marginellus*, *lateralis*, *flavicollis*, *leucocephalus*, *quadrimaculatus*, *leucophthalmus*), but very little was known about its ecology and practically nothing about its colour morph frequencies.

The main objective of the present study was thus to make an introductory analysis of the morph frequencies of the meadow spittlebug in Portugal. Moreover, the habitat effect in the colour polymorphism was also tentatively investigated.

Material and methods

A littoral area at Fontanelas (Sintra), north of Lisbon, was selected as the study field. The material was collected by the junior author at three sites with different vegetation types during 1988. The sites fall within a small area of less than 7,000 m² and the samples were taken from three different vegetation types as defined here: habitat A (open abandoned field), with *Trifolium* spp., *Rumex* spp., *Ononis natrix*, etc.; habitat B (*Ulex*-type pine woodland), a cool *Pinus pinaster* woodland with a shrub community dominated mostly by *Ulex europaea*; and habitat C (*Ononis*-type pine woodland), a warmer *Pinus pinaster* woodland with a shrub community mostly with *Ononis natrix*. The study material consisted of a total of 7,967 specimens, 4,354 males and 3,613 females (table 1).

Sampling was carried out with a standard sweeping net and a "pooter" and, as a rule, under similar conditions at all three habitats. For each habitat and sample session a total of three hours of collecting effort was always given.

However, the total collecting effort was not the same for each of the three habitats: five samples were taken from habitat

A (in March, April and May), three samples from habitat B (in April, May and September) and six samples from habitat C (in April, May, June, July and September). As such, only comparable samples (at the same or similar dates) were used in the statistical analyses (tables 1, 2) and the results presented here should be seen as introductory. For the 2x2 contingency table analysis, the colour morphs were simplified and all three habitats were included at once in order to avoid over dispersion of the data. Moreover, only the females were analysed, since melanic forms for males were poorly represented. Without such modification, most cells would be expected to have frequencies less than five. Data was analysed with G-test (CRAWLEY, 1993). The new categories were: TYP group (POP + TYP), phenotype TRI, and melanics (MAR and LAT morphs, and LCE and LOP groups).

Results

Morph distribution

As referred to earlier, a total of 7,967 specimens of the meadow spittlebug (4,354 males

and 3,613 females), comprising eleven different morphs, were collected at Fontanelas (table 1). The colour morphs encountered, with frequencies for males and females, respectively, were: POP, 39%, 27%; TYP, 57%, 62%; TRI, 3.7%, 4%; MAR, 0%, 3.3%; LAT, 0%, 0.2%; FLA, 0.8%, 1.7%; GIB, 0.07%, 0.06%; UST, 0.02%, 0.03%; QUA, 0.05%, 1.61%; ALB, 0%, 0.08%; and LOP, 0%, 0.17%). Of these, the phenotypes LAT, GIB, UST, ALB and LOP were very poorly represented and the phenotypes VIT, PRA and LCE were absent from the whole collection (tables 1, 2).

Figure 2 depicts the colour morph frequencies for all males and females according to the grouping explained earlier. For males and in decreasing order of frequency the following morph groups and morphs proper were collected: TYP group (95.38%), TRI group (3.70%), LCE group (0.85%), and LOP group (0.07%); for females the order was TYP group (88.79%), TRI group (4.01%), MAR (3.32%), LOP group (1.88%), LCE group (1.74%) and, finally, LAT (0.25%). It is interesting to note that with respect to the TRI morph, a similar value of about 4% was found for both sexes. As expected, the TYP group was more frequent in males than in females (about 95% and 89%, respectively).

Table 2. Frequencies of morphs and groups of morphs (*) of *Philaenus spumarius* for both sexes at Fontanelas (Sintra, Portugal) during 1988. (For abbreviations see the text.)
Frecuencias de morfismos y grupos de morfismos () de Philaenus spumarius para ambos sexos en Fontanelas (Sintra, Portugal) durante 1988. (Para abreviaturas ver el texto.)*

	Sex	Frequencies (%)					
		TYP*	TRI*	MAR	LAT	LCE*	LOP*
Habitat A	M	95.93	3.30	0	0	0.77	0
	F	88.66	3.25	3.70	0.56	2.02	1.80
Habitat B	M	98.50	1.50	0	0	0.00	0
	F	80.12	3.11	4.97	0	3.73	8.07
Habitat C	M	95.11	3.89	0	0	0.91	0.09
	F	89.38	4.33	3.08	0.16	1.52	1.52
Habitat A+B+C	M	95.38	3.70	0	0	0.85	0.07
	F	88.79	4.01	3.32	0.25	1.74	1.88

Moreover, most melanic morphs were as a rule exclusively (MAR, LAT, ALB and LOP) or better represented (FLA, QUA) in females than in males (table 1, fig. 2).

The habitat effect

Lumping the data in table 1, an independence in the distribution of the colour morph categories in the three habitats in 24-25 April was found ($G = 7.74$, d.f. = 4, n.s.). When analysing the 22-29 May data, 17.9% of the specimens in habitat B, 10.4% in habitat A, and 6.88% in habitat C were melanic, the three habitats differing in the female colour morph composition ($G = 9.27$, d.f. = 4, $p = 0.05$).

Such differences among different habitats were especially evident in habitat B and in respect to the LOP (UST + QUA + ALB + LOP) and LCE (FLA + GIB) melanic groups (fig. 3). The following frequencies for females were obtained: habitat A - LCE = 2.02%, LOP = 1.8%; habitat B - LCE = 3.73%, LOP = 8.07%; habitat C - LCE = 1.52%, LOP = 1.52%. Considering

now the total female melanic phenotypes and melanic groups (phenotypes MAR, LAT and LCE and LOP groups), the frequencies for each habitat are as follows: habitat A = 8.2%, habitat B = 16.8 %, and habitat C = 6.3% (fig. 4). This shows clearly that the melanic morphs were comparatively more frequent in habitat B than in the remainder.

On the other hand, the occurrence of the TYP group is dominant for both males and females, as expected, with only small differences among the three habitats: habitat A - males = 95.93% , females = 88.66%; habitat B - males = 98.50%, females = 80.12%; and habitat C - males = 95.11%, females = 89.38%.

Some differences were also found as regards the general diversity of the colour morphs and for both sexes in the habitats here studied. In fact, habitat A proved to have all eleven female colour morphs found in Fontanelas, but failed to have in respect of males the morphs MAR, LAT, GIB, UST, QUA, ALB and LOP. In the case of habitat B, characterized by having the largest percentage of melanics, the morph diversity appeared

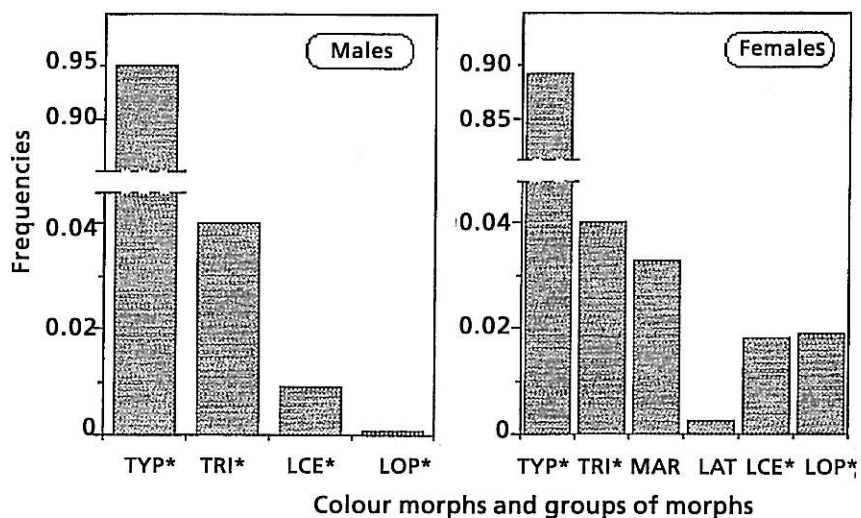


Fig. 2. Male and female colour morph and groups of morphs (*) frequencies of *P. spumarius* in Fontanelas (totals for 1988). Morphs are grouped as in figure 1.

Frecuencias de morfismos y grupos de morfismos () de color en machos y hembras de P. spumarius en Fontanelas (totales para 1988). Para los grupos de morfismos ver la figura 1.*

somewhat impoverished since several morphs were missing, viz. LAT, GIB and UST for females and MAR, LAT, FLA, GIB, UST, QUA, ALB, and LOP for males. This is probably a size effect of the sampling since, as referred to previously, the collecting effort was greater in habitats A and C than in B. Finally, habitat C was characterized by the presence of nine female colour phenotypes (only the rare UST and ALB are missing), and by the absence of the male phenotypes MAR, LAT, ALB and LOP (cf. table 1).

Discussion and conclusions

As a result of a number of studies (e.g. HALKKA et al., 1967, 1976, 1980; HALKKA, 1988; THOMPSON, 1973, 1988), the biological role of the colour polymorphism of *Philaenus spumarius* (L.) is better understood, although details of how the polymorphism is maintained still remain elusive (STEWART & LEES, 1996). The universality and temporal stability of this polymorphism strongly suggest the influence of some sort of natural selection. Several components for the selection regime of the meadow spittlebug have been put forward by the several authors (e.g. HALKKA, 1988; HALKKA & HALKKA, 1990) namely, visual (mainly apostatic and/or aposematic), multiniche selection, and climatic (including the climate-related thermal selection). Owing to the polymorphism's striking vision nature of the meadow spittlebug, predation by apostatic selection has frequently been proposed as the main selective factor (CLARKE, 1969). Thus, polymorphism would be maintained by predation during the relatively long life of the adult, with predators concentrating on hunting the commonest colour phenotype until it has become difficult to find and then switching to the next commonest morph and so on, therefore starting with the non-melanistic (mostly males) like the group TYP and ending with the rarer melanics (mostly females) The males, unnecessary for the population after copulation and often expressed in the most frequent phenotypes (e.g. TYP group, totalling about 95% in most populations), are the principal candidates to be first eaten, therefore protecting their offspring in the form of eggs within females and the females themselves. These are rarer

than males and need protection during a preoviposition period which lasts 4-5 weeks (HALKKA, 1988). This visual hypothesis has also been presented in conjunction with an aposematic model, where a learning predator would recall more vividly a frustrating encounter with a melanistic morph than with a lighter form. To the degree that such encounters lead predator to shun the dark phenotype more than other colour forms, selection will favour such dark form. If as the dark form becomes more frequent in a population the selective disadvantage of being common begins to outweigh the advantage of being conspicuous, a balanced polymorphism would result (THOMPSON, 1973). However attractive the visual model might be, there is lack of evidence demonstrating important rates of predation either by invertebrates or vertebrates (e.g. BERRY & WILLMER, 1986). Therefore, types of selection pressure other than mere visual selection through predators are also probably involved. Multiniche selection is another component recently advanced by HALKKA (1988). It implies that the different colour morphs are also dissimilar ecophysiologically, therefore behaving as sympatrical ecomorphs. These ecomorphs show variable degrees of ecological specialization: rare morphs would occupy small niches and the broader the niche available, the more frequent the morph using a fraction of the habitat. Therefore, morph frequencies would be adjusted according to availability of different types of niches. There are several studies giving some support to this hypothesis, namely the observation that morph frequencies are related to the floral diversity of the habitat (e.g. RAATIKAINEN et al., 1977). Finally, the role of climatic factors is suggested by latitude clines in morph frequencies that have been recognized in Europe and in North America (e.g. HALKKA et al., 1974, THOMPSON, 1984a), with most melanistic forms tending to increase from south to north. This has been explained as being related to the so-called thermal selection, where dark forms will be at an advantage in lower sunlight intensities, and have also found support in some studies along altitudinal transects (e.g. BERRY & WILLMER, 1986; THOMPSON, 1988). Thus darker morphs are more common in cooler areas because, as they warm more rapidly through absorp-

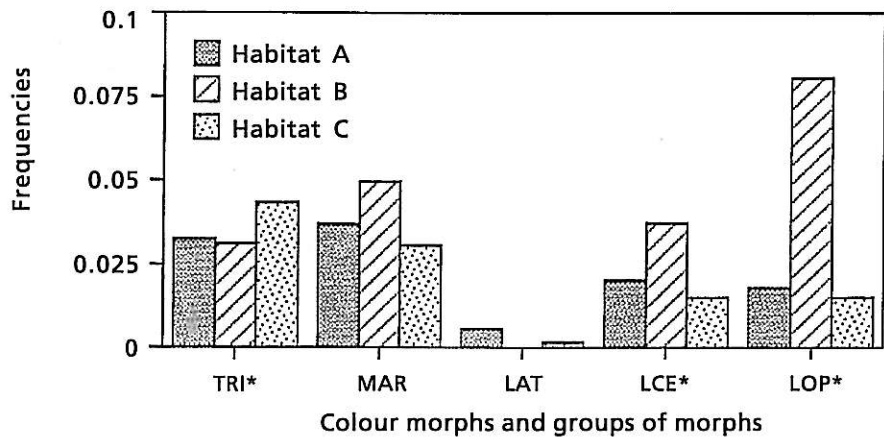


Fig. 3. Frequencies of female rare colour morphs and groups of morphs (*) of *Philaenus spumarius* in the three habitats at Fontanelas in 1988.

Frecuencias de morfismos y grupos de morfismos de color raro en hembras de Philaenus spumarius en los tres hábitats de Fontanelas en 1988.

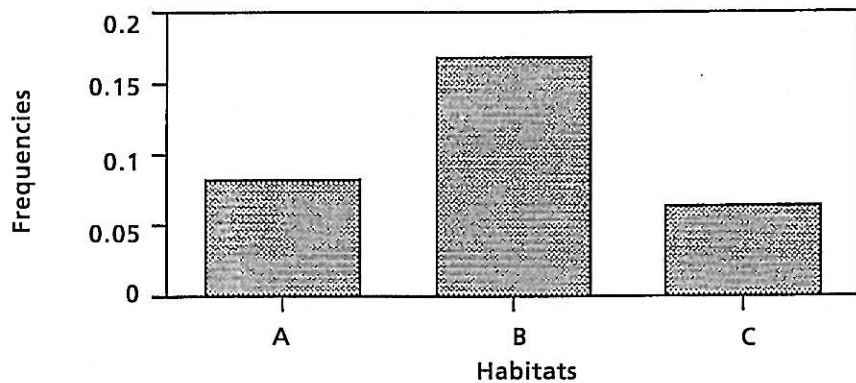


Fig. 4. Female melanic morph frequencies (phenotypes MAR, LAT, and LCE and LOP groups) at Fontanelas in 1988.

Frecuencias de morfismos melánicos en hembras (fenotipos MAR, LAT y grupos LCE y LOP) en Fontanelas en 1988.

tion of incident solar radiation, they gain a relative advantage in feeding, ovipositing and escaping from predators when ambient temperatures are low (THOMPSON, 1984a).

The main purpose of the present study was first to investigate the diversity and frequencies of the colour phenotypes of *Philaenus spumarius* in a littoral area of Portugal (Fontanelas, Sintra), since very little data was available in the Iberian peninsula on this insect. The meadow spittlebug however must be one of the most widely distributed and successful species in the northern hemisphere. Furthermore, a first attempt was made to find out whether the habitat has any effect on the morph frequencies of this species. As stated earlier, the results here reported have shown that eleven different morphs are present in Fontanelas: POP, TYP, TRI, MAR, LAT, FLA, GIB, UST, QUA, ALB, and LOP.

Of the common phenotypes generally encountered by authors only phenotypes VIT, PRA and LCE proper were not found. On the other hand, of the phenotypes previously known from Portugal, only LCE and PRA were not collected in Fontanelas. Moreover, phenotypes LAT, GIB, and UST are new forms to Portugal. As a result, the following thirteen phenotypes are now known to be present in this country: POP, TYP, TRI, PRA, MAR, LAT, FLA, GIB, LCE, UST, QUA, ALB, and LOP. Therefore, only the phenotype VIT still remains to be found in Portugal. From this study it also appears that although the three habitats are contiguous, therefore without offering great barriers to the inter-habitat dispersal by the meadow spittlebug, different colour morph combinations were present in the different habitats, a result in keeping, for instance, with HALKKA et al. (1976) or BOUCELHAM & RAATIKAINEN (1984). In fact, the three habitats appeared to differ in the female colour morph composition. Moreover, habitat B proved to be characterized by the highest frequencies of the melanic morphs. As this is the coolest of the three habitats studied, our data support the thermal hypothesis of selection (e.g. THOMPSON, 1984a, 1988), which as referred to before, predicts that dark forms will be at an advantage in relatively low sunlight intensities and at a disadvantage (due to possible overheating) in relatively high intensities. Higher melanic frequencies would therefore be expected in cooler areas.

However, the present study throws little light on the other factors that may be involved in the selection regime of the meadow spittlebug at Fontanelas. If it was possible to offer a plausible explanation to habitat B having raised frequencies of the melanic morphs, nothing can be advanced to explain the other differences found on the diversity and frequencies of the different morphs in the different habitats here studied. The causes of these differences are elusive and remain to be established. However, the view that these phenotypes might behave as ecomorphs, as interpreted by HALKKA (1988), is strongly favoured here, since a greater diversity of morphs was found in the habitat with the highest plant species diversity (habitat A).

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