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POPULATION GENETICS OF PHILAENUS SPUMARIUS ON THE ISTRANCA MOUNTAINS: II. POLYMORPHISM AND PHENOTYPE FREQUENCY

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Genetically controlled colour polymorphism of the meadow spittlebug *Philaenus spumarius* in the populations of the Istranca Mountains was investigated. A total of 7,544 spittlebugs, 2,936 females and 4,608 males collected from three different types of deciduous forest were analysed. Four non-melanic – *populi* (POP), *typicus* (TYP), *trilineatus* (TRI), vittatus (VIT), – and four melanic – *marginellus* (MAR), *lateralis* (LAT), *flavicollis* (FLA), *leucocephalus* (LCE) – phenotypes expressed by six different alleles were determined. Melanic phenotypes were limited to the female sex only, moreover the melanic "O" group was not found in the 29 different populations sampled. POP+TYP were predominant phenotypes in the pooled samples (94%). The combined melanics and TRI+VIT were present at equal proportions (3% each). The average sample size for 40 sampling sessions was (Mean±S.E.) 187.1±14.3 (range: 31–361).

Key words: polymorphism, melanism, Homoptera, *Philaenus spumarius*, Turkey

INTRODUCTION

Eight different species have been described in the genus *Philaenus*, and the majority of these are found in Europe (DROSOPOULOS & REMANE 2000, DROSOPOULOS & QUARTAU 2002, DROSOPOULOS 2003). *Philaenus spumarius* (L.) (Homoptera: Cercopidae) is the most well-known spittlebug. It occurs abundantly and has a wide distribution in the Holarctic region (WEAVER & KING 1954, HALKKA & HALKKA 1990, STEWART & LEES 1996).

A considerable body of data on *P. spumarius* has accumulated from mainly ecological studies dealing with its noxious status as an economically important pest for numerous plants (WEAVER & KING 1954, YURTSEVER 2000). Although colour pattern variations of the adults have been noticed earlier (HAUPT 1917), the importance of this polymorphism for genetic and evolutionary studies (HALKKA & HALKKA 1990, STEWART & LEES 1996, YURTSEVER 2000, HALKKA *et al.* 2001) has been understood in the last decades. Thirteen classifiable dorsal colour/pattern phenotypes of the adult *P. spumarius* occur in most natural populations (STEWART & LEES 1996). These are categorised as non-melanics – POP (*populi*), TYP (*typicus*), TRI (*trilineatus*), VIT (*vittatus*) and PRA (*praeusta*) and are light straw coloured with dark mottling, or stripes. The remaining are melanics – MAR (*marginellus*), LAT (*lateralis*), FLA (*flavicollis*), GIB (*gibbus*), LCE (*leucocephalus*), QUA (*quadrimaculatus*), ALB (*albomaculatus*), and LOP (*leucopthalmus*), predominantly black or dark brown with different combinations of pale markings on the dorsal surface. Only eight of these morphs (Fig. 1) occur on the Istranca Mountains, Turkey. Seven alleles at a single autosomal locus are responsible for the expression of a single morph or a group of similar phenotypes (HALKKA *et al.* 1973, HALKKA & HALKKA 1990, STEWART & LEES 1996).

The occurrence and frequencies of the dorsal phenotypes of *P. spumarius* display geographic variations (BOUCELHAM *et al.* 1988, HALKKA & HALKKA 1990, STEWART & LEES 1996) which sometimes may be clinal at the large geographic scale (HALKKA & MIKKOLA, 1965, THOMPSON 1988). Since particular morphs are adapted to different host plants (HALKKA & HALKKA 1990), some variations may be due to microclimatic or edaphic environment differences where various plant species grow (WHITTAKER 1968). Particular local populations can also offer a good example of local genetic adaptation (LEES & DENT 1983) to explore how evolution acts in the fine-grained environments. Several patterns of natural selection (HALKKA & MIKKOLA 1965, LEES & DENT 1983, THOMPSON 1988, HALKKA & HALKKA 1990, STEWART & LEES 1996, HALKKA *et al.* 2001) and genetic drift (BRAKEFIELD 1990, LEES 1993, HALKKA *et al.* 2001) have been most discussed evolutionary components affecting these remarkable variations.

P. spumarius has been recorded from several parts of Turkey (LODOS & KALKANDELEN 1981). Recent report has dealt with the genetic basis of the polymorphism (YURTSEVER 1999), however information on the phenotype frequency regarding the natural populations is very limited (YURTSEVER 2001). Population genetics of *P. spumarius* on the Istranca Mountains, in northwestern Turkey was

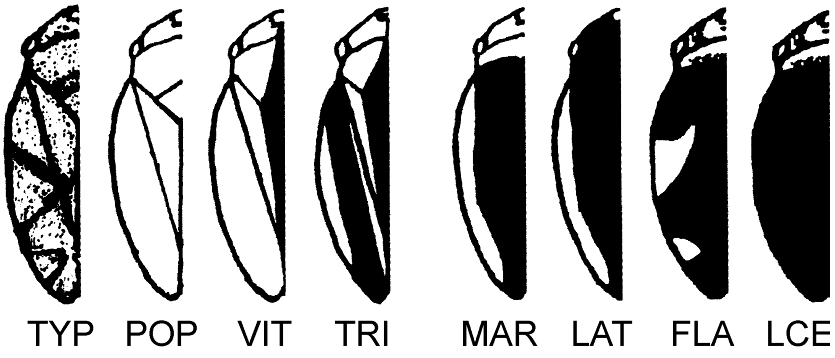

Fig. 1. Dorsal colour/pattern phenotypes of *Philaenus spumarius* found on the Istranca Mountains, Turkey (abbreviations are described in the text)

studied. The phenotypic diversity, allele frequency, sex ratio, and associations between several parameters of the polymorphism and habitats have been investigated. The present paper provides detailed information about the occurrence and frequencies of the dorsal colour/pattern phenotypes in the three different types of forest studied.

MATERIALS AND METHODS

Sampling sites

Three different forests of the Istranca Montains in northwestern Turkey were chosen for the study area. Because each one of these forests is characterised by different deciduous tree species, and therefore are three particular habitats with distinct microclimatic conditions for *P. spumarius.* The three forest types can be described as follow:

(a) Mixed forests – consisted of mixed deciduous tree species such as *Populus tremula*, *Alnus glutinosa*, *Mespilus germenica, Tilia argentea*, *Cornus mas, Cornus sanguinea, Juniperus oxycedrus, Carpinus betulus, Acer campestre* and *Coryllus avellana*.

(b) Oak forests – characterised by various species of the oak (*Quercus* spp.) trees and ferns (*Pteridium* spp.). Oak forests are erroneously called as dry forests in the area, possibly because of they have less average annual precipitation than other types of the forests but these forests are also highly humid providing good living environments for the spittlebugs.

(c) Beech forests – involves most humid study sites and are always cooler but milder than other forests throughout the year. Several beech trees (*Fagus* spp.) and particularly *Rhododendron ponticum* characterise the beech forests.

The sampling sites were entirely rural, undisturbed and unpolluted, providing numerous herbaceous and other favoured host plants for the nymphs and adults of the meadow spittlebugs. The commonest plant species at the study sites were the following: *Ranunculus primula, Rubus fruticosus, Trifolium* spp., *Medicago* spp., *Vicia* spp., *Ilex aquifolium, Hedera helix, Viola silvatica, Veronica officinalis, Hypericum perforatum, Euphorbia* spp., *Primula officinalis, Arrhenatherum elatius, Hordeum murinum* and numerous other gramineous herbs. The sampling of the adult insects was carried out between early July and late October in 2001. The spittlebugs were collected from the plants, sometimes from trees, near the roadsides, streamsides and mini-meadows where they were found abundantly. Each sampling was performed using a standard sweeping net and a hand-held aspirator. Specimens were analysed in the laboratory, under a binocular stereomicroscope. A total of 7,544 adult insects 2,936 females and 4,608 males was collected and examined for dorsal colour/pattern polymorphism (Table 1). Since five of the total 45 samples (n) were small, 7485 insects including 40 samples were used in the major statistical analyses. The scoring of the adult individuals for the dorsal colour/pattern was straightforward, because the observed phenotypes were clearly expressed in all specimens. During the study, about half an hour was spent for each of the 45 sampling sessions.

Statistical analysis

The χ^2 Contingency Test (R × C) was used to compare the types of habitat (LEES *et al.* 1983, FOWLER *et al.* 1998) regarding the categories of the phenotypes where appropriate. Frequencies of the sexes in the three habitats were compared (2 × 3) where appropriate phenotypes are found in both sexes. Comparisons between the types of habitat were applied to the five different phenotype categories in females (2 × 5) and three different categories in males (2 × 3) separately.

RESULTS

In almost all samples, adult meadow spittlebugs were highly abundant in the populations of the Istranca Mountains. During some sampling sessions, it was possible to obtain dozens of insects in only one sweep net action. Therefore sampling sessions rarely took over half an hour. The average number of insects was (Mean±S.E.) 167.6±15.1 (range: 1–361) for 45 sampling sessions. Only five samples included less than 20 insects. If these five samples are ignored, the average increases to 187.1±14.3 (range: 31–361) in the 40 sampling sessions. Eight different dorsal colour/pattern phenotypes that are common in many natural populations of *P. spumarius* were found on the Istranca Mountains of Turkey (Fig. 1). Thus, it seems that there are at least six different alleles – "t, T, M, L, F, and C" – expressing the phenotypes of POP+TYP, TRI+VIT, MAR, LAT, FLA and LCE respectively. On the other hand, the allele "O", responsible for three other melanic phenotypes of *P. spumarius*, was not detected in these Turkish populations. Besides, melanic phenotypes were expressed only in the females but not in the males.

As shown in Figure 2, the predominant phenotype in the females and overall is TYP (54–49% respectively), followed by POP, (34–45%). On the contrary, POP (52%) is higher than TYP (45%) in males. The frequencies of TRI+VIT and combined melanics are much lower than POP and TYP in all categories. Regarding the pooled sexes of *P. spumarius*, TRI+VIT and melanic phenotypes occur equally

Table 1. Summary data for *Philaenus spumarius* colour/pattern phenotype frequencies on the Istranca Mountains, Turkey (Based on 45 samples from 29 different populations in the three types of habitat) Key: Mx – Mixed, Ok – Oak, Bh – Beech, forests

Phenotype	Females			Males			Total
	Mx	Ok	Bh	Mx	Ok	Bh	
POP	247	441	306	499	846	1051	3390
TYP	378	655	570	405	754	900	3662
TRI	24	31	36	27	46	71	235
VIT	4	4	8	3	3	3	25
MAR	39	53	53	0	0	0	145
LAT	6	6	6	0	0	0	18
FLA	16	20	26	0	0	0	62
LCE	2	2	3	0	0	0	7

(3% for each) on the Istranca Mountains, even though there is a lack of melanics in the male sex.

Since there were no melanic males in the habitats examined in the present study, it was only possible to compare the frequency distributions of the phenotype groups separately in the females and the males (Fig. 3).

It is clear that in all of the three types of the habitat, frequencies of the females and the males tend to be different (P 0.001) regarding POP, TYP, and TRI+VIT. Because the males have higher frequencies than the females in all of the three phenotype categories. Five phenotype categories in the pooled data (Fig. 3) are also comparable to see the frequency differences between the three types of habitat (Table 2). Statistically significant difference occurs only between the oak and beech forests in the female sex. The pattern of distribution for these two categories of the habitat regarding the females respectively is: 30–36% POP, 57–54% TYP, 4–3% TRI+VIT, 6–5% MAR+LAT, 3–2% FLA+LCE. Comparisons within the three types of habitat concerning the males of the five different phenotype categories reveal no sign of differences. Thus, there is a tendency that the three types of habitat exhibit a very close resemblance in the phenotype distribution. As a result, it can be concluded that all of the three types of habitat on the Istranca Mountains are characterised by high frequencies of POP and TYP, but low frequencies of both TRI and melanic phenotypes of *P. spumarius*.

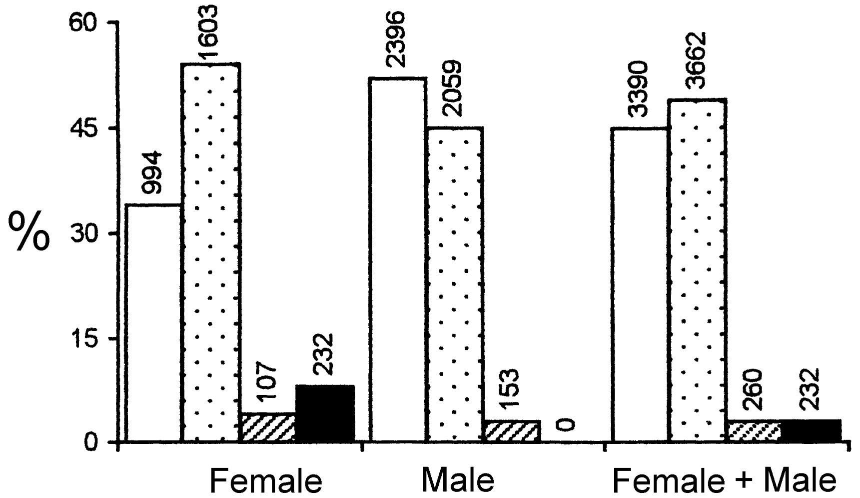

Fig. 2. The chart for the combined four major phenotype categories of *Philaenus spumarius* showing the frequency distributions on the Istranca Mountains, Turkey. From left to right, three groups of bars blank, dotted hatched, and dark coloured bars of the diagrams indicate POP, TYP, TRI+VIT, and melanic (MAR+LAT+FLA+LCE). The height of the bar indicates the percentage (numbers are given at the top)

Table 2. Comparisons between the categories of habitat in Fig. 3, using the χ^2 contingency test. Comparisons for females (2 × 5) and males (2 × 3) are presented separately. Two asterisks indicate significance at the 0.01 probability level, and N. S. not significant at 0.05 level

		Oak	Beech
Female	Mixed	4.757 (N. S.)	3.849 (N. S.)
	Oak		13.651 (**)
Male	Mixed	1.370 (N. S.)	0.809 (N. S.)
	Oak		1.659 (N. S.)

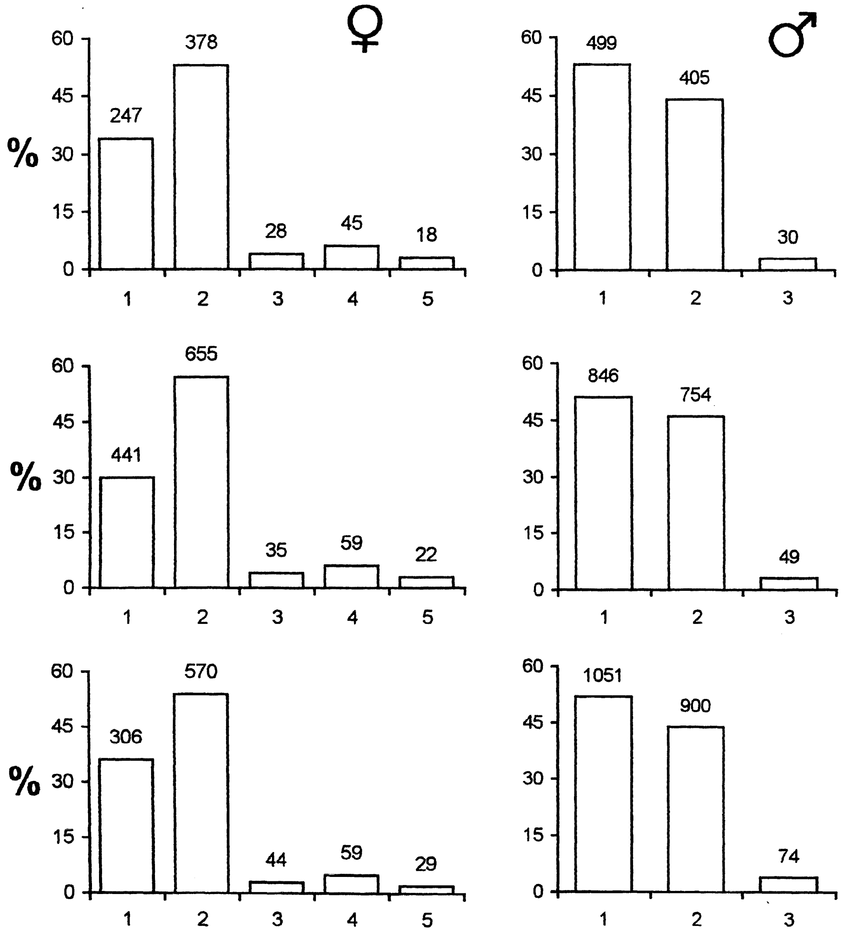

Fig. 3. Combined phenotype frequency distributions of *Philaenus spumarius* for three types of habitat on the Istranca Mountains, Turkey. Separate diagrams for females and males denote the habitats from top to the bottom: Mixed, Oak, and Beech forests respectively. From left to right, the bars of the diagrams indicate; 1: POP, 2: TYP, 3: TRI+VIT, 4: MAR+LAT, 5: FLA+LCE. The height of the bar indicates the percentage (numbers are given at the top)

DISCUSSION

Only eight of the most common eleven phenotypes (HALKKA & HALKKA 1990, STEWART & LEES 1996, YURTSEVER 2000) of *P. spumarius* occurred in the populations of the Istranca Mountains. The "O" group phenotypes were not detected in these Turkish populations. The findings presented here are similar to the results of a recent report (YURTSEVER 2001) dealing with the *P. spumarius* populations of Turkish Trakya where only two melanics, the FLA and MAR have been detected at low frequencies. In the studied New Zealand populations, the number of the alleles may be as low as two (YURTSEVER 2002), responsible for three (LEES 1993) or four (HODGE & KEESING 2000) different phenotypes. Samples of QUARTAU and BORGES (1997) have not included any of the VIT, PRA and LCE phenotypes over 7,500 specimens obtained from Portuguese populations. WHITTAKER (1972) and VILBASTE (1980) reported only TYP and POP (allele "t") from Kamchatka.

As in previously studied populations of Turkish Trakya, the melanic phenotypes of the meadow spittlebug were entirely restricted to the female sex in the populations of the Istranca Mountains. Absence or rarity of certain melanic phenotypes in the males, has also been reported in several populations in Europe (HALKKA 1964, WHITTAKER 1972, HONEK 1984, QUARTAU & BORGES 1997, HALKKA *et al.* 2001) and North America (THOMPSON & HALKKA 1973, BOUCELHAM *et al.* 1988). In fact, in all of these studies, a number of the melanic males has always been presented, even if at the low frequency. Entire deficiency of the melanic alleles in the male sex has also been demonstrated in some other Turkish populations (YURTSEVER 2001). Only in certain local British populations, the melanics are fully expressed in both sexes (STEWART & LEES 1996). It has been suggested that (HALKKA *et al.* 1980, STEWART & LEES 1996, YURTSEVER 1999) the limitation of certain phenotypes to one sex may be due to the geographic variations of some other genetic loci, influencing the main locus of the polymorphism concerned. The significance of these kind of genetic interactions for the evolution of polymorphism has also been stated in some other polymorphic species such as, the spider *Enoplognatha ovata* (OXFORD 1989), land snail *Cepaea nemoralis* (JONES *et al.* 1977) and several Lepidoptera (CLARKE & SHEPPARD 1971, MIKKOLA 1984). The precise reason for the deficiency of the melanics in the male sex regarding the populations of Istranca Mountains remains to be unclear. The progressing laboratory genetic work with *P. spumarius* will probably shed light to understand this situation. As reported here, melanic phenotypes of *P. spumarius* occur at low frequencies in the vast majority of the populations previously studied. Combined non-melanics in the populations of Istranca Mountains were over 95% regarding the pooled data. Thus, predominant phenotypes were POP+TYP which accounted over 90%. Similar patterns of frequency distributions regarding the proportions of melanics and non-melanics occur in the majority of *P. spumarius* populations. A few examples may sharply deviate from the pattern discussed above. For example, in certain local populations in the U. K. (LEES & DENT 1983), frequencies of melanics may be up to 95%. Therefore, comparable variations between different natural populations may often occur. These variations may arise as an industrial melanism due to rapid genetic adaptations to changing environmental conditions (LEES & DENT 1983). The local population variations in the phenotype frequency are sometimes attributed to apostatic selection (OWEN & WIEGERT 1962) by a variety of predators. Also, microclimatic factors in some cases may generate associations between the phenotype frequency and a specific type of habitat (QUARTAU & BORGES 1997). However, such influences may not be traced in certain populations (THOMPSON & HALKKA 1973, HONEK 1984, HODGE & KEESING 2000). At the large geographic scale, the evidence of such deterministic elements on this polymorphism may be detected more clearly. In this respect, it has been proposed that the level of melanism is highly correlated with thermal factors (BERRY & WILLMER 1986, THOMPSON 1988). In cooler places, such as at northern latitudes (HALKKA & MIKKOLA 1965, WHITTAKER, 1972) and higher altitudes (BOUCELHAM *et al.* 1988), melanic forms may take advantage with their darker body colours (KETTLEWELL 1973). Thus, they may increase their frequencies in respective environments. In the *P. spumarius* populations of Istranca Mountains, significant differences in the phenotype frequency occurred between the oak and beech forests. Although it is too early to make any conclusion influencing this differentiation, it may be assumed that certain phenotypes of *P. spumarius* may have adapted to beech forests better than oak forests. Because beech forests may have provided more humid places for the better survival of mentioned forms.

On the other hand, particular role of stochastic events which has already been suggested for several populations (BRAKEFIELD 1990, LEES 1993, HALKKA *et al.* 2001, YURTSEVER 2001) of this homopteran may be examined in the Istranca Mountain populations of *P. spumarius*. The lack of the allele “O” in the populations presented here and in previously studied Turkish populations (YURTSEVER 2001) is striking. On the Carpathian Mountains, about 700 km NW of the Istranca Mountains, this allele is much more common than the adjacent lowlands (HALKKA *et al.* 1980). Thus, the evolution and geographic distribution of the allele “O” (HALKKA & HALKKA 1990) and the other melanic alleles have yet to be elucidated in detail. Since there are no previous data dealing with these populations, the information available for the discussion of evolutionary agents acting in the *P. spumarius* populations of the Istranca Mountains is very limited. In conclusion, the colour/pattern polymorphism in the meadow spittlebug *P. spumarius* remains to be one of the subtle phenomena for the study of evolution in action.

*

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