

On the Polymorphic Meadow Spittlebug, *Philaenus spumarius* (L.) (Homoptera: Cercopidae)

Selçuk YURTSEVER

Trakya University, Faculty of the Arts and Science, Department of Biology, 22030 Edirne - TURKEY

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Abstract: Due to its interesting biological aspects, the meadow spittlebug *Philaenus spumarius* has received great attention from biologists for decades. It has been one of the extensively studied species in ecology and genetics. This homopteran insect shows very high habitat diversity and therefore has a wide global distribution. Adults exhibit a heritable colour/pattern polymorphism on the dorsal surface throughout its range. A similar colour/pattern variation also occurs in certain ventral parts.

Recent laboratory studies have dealt with its polyandrous aspect that is, females may mate several times with different males and the offspring of a single female may be fathered, therefore, by several males. Although the effects of multiple mating on natural populations of *P. spumarius* are not well known, it may have great evolutionary importance through increased genetic heterogeneity and high fitness.

Key Words: Meadow spittlebug, *Philaenus spumarius*, Homoptera, Cercopidae, polymorphism, melanism, genetics, polyandry

Polimorfik Çayır Köpük Böceği, *Philaenus spumarius* L. (Homoptera: Cercopidae) Üzerine Bir Derleme

Özet: Çayır köpük böceği olarak bilinen *Philaenus spumarius*, ilginç biyolojik özelliklerinden dolayı uzun yıllardır biyologların büyük ilgisini çekmiştir. Bundan dolayı ekoloji ve genetikte en çok çalışılan türlerden birisi olmuştur. Bir homopter olan bu böcek çok çeşitlilikli habitatlarda yaşayabildiğinden dünyada geniş bir dağılıma sahiptir. Erginleri bütün dağılım alanında, genetik olarak kontrol edilen dorsal renk ve desen polimorfizmi gösterir. Benzer bir renk ve desen varyasyonu aynı zamanda ventral yüzeyde de görülür.

Yakın zamanda yapılan laboratuvar çalışmaları, bu türün poliandri ile ilgili özelliklerini ortaya koymuştur. Dişi *P. spumarius* bireyleri yaşam devrelerinin üretme periyodunda birden fazla erkekle defalarca çiftleşebilir. Sonuçta tek bir dişiden bir defada meydana gelen yavruların babaları farklı olabilir. Poliandri'nin bu türün doğal populasyonlardaki evrimsel ve diğer etkileri tam olarak bilinmemekle beraber, bu davranış *P. spumarius* populasyonlarında genetik çeşitliliği artırtır ve dolayısıyla bu türün evrimsel başarısında önemli bir faktör olabilir.

Anahtar Sözcükler: Çayır köpük böceği, *Philaenus spumarius*, Homoptera, Cercopidae, polimorfizm, melanizm, genetik, poliandri

Introduction

Spittlebugs and their nymphal protection have received attention from biologists for centuries. Interesting theories have been proposed for the origin of spittlemasses found on plants in spring. The cuckoo bird has been suggested as a reason, since this summer migrant appears in Europe at the same time as the first spittle masses (1). Therefore this theory gives rise to the name cuckoo-spit insects. In the literature, spittlemasses have been called Gowk's spittle, frog spit, toad spit, snake spit, witch's spit and wood sear. It has also been suggested that some plants are able to produce spittle

masses. It has even been cited that spittle masses generate small locusts (2).

It is now known that the spittle masses that are seen on many plants in spring are produced by the nymphs of the spittlebugs in the family Cercopidae, which surrounds their delicate soft body and gives them some protection from predators and desiccation. The spittlebugs are homopteran bugs in the superfamily Coccoidea. This group currently contributes approximately 2380 species to the Homoptera (3), and all are "xylem-feeders" and "phloem-feeders" both as nymphs and adults (4). They occur on almost all types of plants. Since the nymphs live

in masses of froth, they are commonly called spittlebugs, but are also known as froghoppers from their adult leaping ability (5). The nymphs derive their nourishment from xylem elements by piercing them with their stylets and sucking the sap. The spittle is derived from fluid voided from the anus and from a surfactant secreted by epidermal glands on the seventh and eighth abdominal segments. Air bubbles are introduced into the spittle by means of the caudal appendages of the insect (6). A spittlebug nymph usually rests head downward on the plant, and as the spittle forms, it flows down over and covers the nymph, providing the nymph with a moist habitat. Adults are free living individuals and do not produce spittle.

There are ten British Cercopid species producing spittle (1), and three European species are known in the genus *Philaenus* (7,8). *P. signatus* and *P. loukasi* are two of these. The third *P. spumarius* is the most abundant, and is usually known as the meadow spittlebug. There is a large body of literature about it, dating from late sixteenth century (2). The studies dealing with *P. spumarius* can be grouped into two categories. The first category involves surveys of its noxious effects as a serious pest on cultivated and wild plants. The second category involves surveys of the colour/pattern polymorphism of populations from different geographic areas, since adults of the meadow spittlebug exhibit great colour/pattern variations, both in wing markings and the colour and pattern of the ventral parts.

In recent decades the meadow spittlebug *P. spumarius* has increasingly become one of the most studied species on various aspects of biology, since it is very suitable for genetics, ecology and other population studies. This review emphasises its importance based on the information obtained from previous surveys and my own study.

Ecology

Habitat and host plants

Owing to its highly polyphagous nature and flexibility, *P. spumarius* occurs in most terrestrial habitats (9,10). Nymphs and adults are found on various plants in habitats moist enough to provide them with sufficient moisture to keep them alive, such as meadows, abandoned fields, waste ground, roadsides, streamsides, also forests, hayfields, marshlands, parks, gardens and cultivated fields.

Hundreds of host plants of *P. spumarius* have been recorded from North America (2,11), New Zealand (12), Hawaii (13) and Europe (14-18). These plants range from grasses to trees, including meadow crops, herbs, thistles, garden plants, shrubs, even conifers. Dicotyledonous plants tend to be used more often than monocotyledonous plants (14,17).

Nymphs and adults feed on nearly all parts of the plants above soil level, but principally on actively growing parts (e.g., leaves, stems, flowers and fruits) (19,20). Nitrogen fixing herbaceous legumes and some other plants which have a high amino acid concentration in the xylem sap (*Medicago sativa*, *Trifolium* spp., *Vicia* spp., *Xanthium strumarium*) are most favoured (21). These hosts provide a relatively rich source of nitrogen compounds as nutrition in the xylem (21,22). It has been pointed out that nitrogen is a limiting factor for some feeding behaviour in *P. spumarius* (23) and therefore it may be a selective advantage for individual insects, which feed on the most nutritious plants.

Geographic distribution and economic importance

It is suggested that humidity is a vital climatic factor determining the distribution limits of the meadow spittlebug in all stages of its survival, therefore an environment that has an abundant water supply for the plants with high humidity is usually favourable (2). Although the meadow spittlebug is one of the commonest insects and has a very wide world distribution, it does not occur in most arctic, alpine and arid zones, because temperature is another factor limiting its distribution (9). For example, the egg hatching and nymphal development stages of *P. spumarius* are temperature dependent (24), moreover, adults may die above and below certain temperature limits (9).

P. spumarius has been recorded from different latitudes and altitudes in much of the Palearctic and Nearctic regions (15,25-27). Its distribution ranges from north Lapland to the Mediterranean in Europe (9,10,16,28,. It has been reported from north Africa (7), several parts of the former Soviet Union (29-32), as well as Afghanistan (33) and Japan (34). It has been surveyed in the U.S.A. and Canada where it has been introduced and is an important pest (2). Its global distribution also covers the Azores (35), Hawaii and New Zealand in the Southern Hemisphere where it has been accidentally introduced in the last few decades (12,13,17,36,37). Recent records involve Turkey (38,39,40,41).

In Europe, *P. spumarius* is not considered a serious pest and rarely causes severe damage (42,43). It has been, however, regarded as an economic pest of crops and other cultivated plants in America. It mainly causes two types injury to plants.

The first type of injury is as a vector of some plant diseases. It has been stated that *P. spumarius* transmits the virus of Pierce's disease of grapevines from diseased to healthy vines and some other plants, which may serve as reservoirs of the virus (44). It has also been mentioned that the species may be a vector of peach yellows and little peach disease, and may be a carrier of the plum mite (19).

The second type of injury is its directly harmful effect on plants. The nymphs cause the main injury. *P. spumarius* nymphs may take up to 280 times their own fresh weight of the plant sap in 24 hours (22). Heavy infestations of the nymphs and adults on plants cause serious damage, leading to reduction and losses in crop yield. *P. spumarius* is an economically important pest of alfalfa (*Medicago* sp.) (45-47), goldenrod (*Solidago* sp.) (48,49), clovers (*Trifolium* spp.) (36), and strawberries (*Fragaria* spp.) (19,50). Spittlebug injuries weaken the infested plants and cause significant deformation which results in delayed plant maturity and reduced forage yield. Damaged fields give relatively poor second-crop yield and the effects of the injuries may even persist to affect yield in the following year.

Population densities of *P. spumarius* may be variable but often can reach very high densities in suitable habitats, hence its pest status. Peak densities of 1280 nymphs/m² and 466 adults/m² have been recorded from some alfalfa fields (20). The same author has also cited densities of 6680 nymphs per m². However, the nymphal densities usually remain under 1000 nymphs/m² and are rarely recorded over this value in Europe (50).

As a result, it can be said that damage of the meadow spittlebug to crops and other plants seems quite significant. However, some of these effects may have been overestimated. It has been shown that resistant cultivars to *P. spumarius* can be found in most alfalfas (51), goldenrods (52) and some other wild and cultivated plants (53). In addition, effective pesticides and natural enemies play a significant role in regulating its population density (19,42,54).

Natural Enemies

Although there is a lack of detailed information concerning natural enemies, several vertebrates and invertebrates have been reported to attack adults, nymphs and eggs of the meadow spittlebug. Harper and Whittaker (55) released *P. spumarius* specimens after labelling them with a radioactive isotope and then they determined the potential predators by scanning their levels of radioactivity.

Birds are important predators of the meadow spittlebug. For example, Evans (56) analysed the contents of the gizzards and faecal pellets of sparrow species *Pooecetes gramineus*, *Spizella pusilla* and *S. passerina* and found that their diet contained *P. spumarius* during the breeding season. Halkka and Kohila (57) summarised a list of some other common bird predators of the meadow spittlebug from different authors. These include two gallinaceous species *Tetrao urogallus* and *Phasianus colchicus* that appear to feed on the nymphs. Other species *Perdix perdix*, *Delichon urbica*, *Corvus frugilegus*, *Turdus viscivorus*, *T. philomelos*, *Phylloscopus trochilus* *acredula* and *Sturnus vulgaris* in the list are predators of adults.

The common frog, *Rana temporaria* is another vertebrate predator of the meadow spittlebug (58). It has been shown that adult *P. spumarius* appear as the commonest cercopid in the diet of this frog in Ireland in September.

Several Arachnids, Hymenoptera, Diptera, and Coleoptera have been reported as invertebrate predators of the meadow spittlebug. In particular, *Mitopus morio* and some other spiders have been shown as predators of adults (55,59). In addition, the prairie ant, *Formica montana*, has been reported to prey on *P. spumarius* nymphs (60).

P. spumarius has several parasitic enemies. Adults are attacked by the dipteran parasitoid *Verrallia aucta* (42), and by the Nematode *Agameris decaudata* (2). Furthermore, an entomophagous fungus of the genus *Entomophthora* attacks adults (42). Some Hymenoptera *Ooconus* spp., *Tumidiscapus* sp., *Centrodora* sp. and dipterans are known as egg parasitoids (2).

Life Cycle

P. spumarius is known as a univoltine and hemimetabolous insect in most of its range (61), although Drosopoulos and Asche (27) believed that the

species may be partly bivoltine in certain parts of Greece. British and some Turkish *P. spumarius* populations are univoltine (10,18). After the overwintering, egg hatching begins in April. There are five nymphal instars and adults appear in June. Adults start to mate soon after the final eclosion, and copulating pairs can be seen throughout the summer. Adults exist at least until October. However, as the summer season advances the number of males declines in proportion to females (61), since males generally do not survive as long as females (10). Oviposition commences in early September, females are induced to lay eggs by the short daylight and the low temperature, and then eggs undergo overwintering diapause. Before the hatching in spring, this diapause is broken by exposure to a chill period – which is less than 5°C – of about 100 days (62).

There are certain temperature thresholds, which play an important role on the egg hatching and nymphal developmental stages (24,50), that temperature influences could modify the egg hatching and developmental rates of these periods. The low temperature causes severely delayed development of the nymphs (63). Development to adulthood requires a sum of 700-800 day-degrees above 5°C (9). Hence, in cooler climatic conditions development to the adult stage takes longer. Adult mortality, therefore, in such areas begins earlier owing to frost. Finnish Lapland is the northern limit of the species' distribution; nymphs may last up to mid-August but sometimes are killed by the first autumn frost (9). In western Turkish populations, adults disappear earlier than northern European populations, due to dry summer conditions (Yurtsever, unpublished data).

Hawaii is the only tropical area where this species is recorded, but it is restricted to the cooler highland sites (64,65). In Hawaii, however, there is no clear pattern of seasonality for the life cycle, since the day-length remains at about 12 hours throughout the year (13,17). New Zealand is probably the southern limit of the species. Accordingly, in New Zealand, the life cycle of the species has shifted by six months parallel to the seasonality of the Southern Hemisphere (37).

The phenology of the life cycle of *P. spumarius* may be different in certain parts of its global distribution, because the species encounters an extensive range of climatic conditions due to its wide distribution. However, variations of the life cycle are not fundamentally different

(2,9,11,17 27,37,42,66). In North Europe, gravid females begin to lay eggs in late summer. The number of the eggs laid varies but an individual female may produce up to 350-400 eggs (67). The eggs are laid in packets sometimes containing 10-20 eggs held together by frothy cement. In the laboratory conditions, each nymphal stage takes about 10 days, and adults usually appear approximately 50 days after the hatching. The females may mate a few days after emergence. The life cycle is completed by the oviposition stage.

Breeding *Philaenus spumarius* in the laboratory conditions

Owen and Wiegert (68) emphasise that breeding *P. spumarius* in captivity is difficult although several attempts have succeeded (2,11,24,63,69). However, none of them have been performed in real laboratory conditions. Although these breeding studies have dealt with different disciplines, very little attention has been paid to the inheritance of the polymorphism. The majority of these studies have been concerned with the ecology or other non-genetical aspects of the polymorphism.

In contrast, Halkka et al. (70) carried out genetical crossing experiments with Finnish *P. spumarius* in natural habitat conditions. The first laboratory breeding experiments on the inheritance of this polymorphism were carried out with British populations by Stewart and Lees (71), and laboratory culture techniques have been described in detail by West and Lees (62). The long life cycle is one of the difficulties of studying *P. spumarius*. Nevertheless in certain laboratory regimes the life cycle may be shortened to six months (71). This is also confirmed with recent extensive laboratory experiments (18, 67). Thus, in the laboratory conditions, the life cycle of *P. spumarius* can be described as follows.

Eggs

These are about 1 mm long, and 0.35 mm wide, elongated, ovoid and tapering in shape. When first oviposited, the egg is yellowish white and has a dark orange pigmented spot in the shell at one end. If the egg is fertilised this orange spot gets bigger and a black coloured, lid-like formation develops on it in about 90 days (67). This lid-like black formation clearly indicates that the eggs are ready for hatching. The young nymph leaves the egg through the black lid. The black lid does not develop if the egg is not fertilised or if it is unhealthy; the orange spot still remains but the egg turns brown and eventually shrivels. In optimum conditions, hatching takes

place after approximately 20 days and the first instar appears.

Nymphs

There are five nymphal instars. The first instar is light orange when newly emerged. This orange colour gradually turns green from the late first instar to the fifth instar. As the nymph develops some other morphological changes occur also. For example, the body length increases through successive instars and the length of the legs gets longer in proportion to the body length, the abdomen flattens dorso-ventrally. Also wing pads begin to appear in the third instar and they become more visible in the fourth and the fifth instars. In this way, different stage nymphs can be distinguished morphologically from each other. In addition, the fourth and the fifth instars are detected by the larger spittle masses they produce on the host plant. The fourth and the fifth instars may be sexed according to their nymphal external genitalia.

The first instar

The body length is approximately 1.35 mm, when freshly hatched. It is orange and produces little spittle on the host plant. Wing pads and external genitalia are not developed. It is very delicate, and moves slowly.

The second instar

The body length is approximately 2.25 mm and slightly bigger than the first instar, but they can be distinguished from them by their yellowish orange colour. Wing pads and external genitalia are still not developed.

The third instar

The body length is approximately 3 mm and more greenish than yellow. It is clearly distinguishable from the previous instars. In addition, wing pads and external genitalia begin to develop, but still the nymphs cannot be sexed.

The fourth instar

The body length is approximately 4.75 mm and green. Yellowish wing pads are clearly visible and, external genitalia are developed. The fourth instar can be sexed with difficulty under ca x10 magnification.

The fifth instar

The body length is approximately 6.25 mm and green. Yellowish wing pads are well developed, external genitalia can clearly be seen under magnification. They produce a great deal of spittle on the host plant.

Adults

The body length is approximately 6 mm, females are slightly larger than males. In the laboratory conditions, adults emerge approximately 50 days after nymphal stages. Adults usually stay in the spittle mass until the cuticle is hard and fully pigmented. However, they may occasionally leave their spittle mass earlier. Adults are fully mature approximately ten days after leaving the spittle and females may mate several times thereafter.

The colour/pattern polymorphism

The dorsal colour/pattern polymorphism

Adults of *P. spumarius* are polymorphic for dorsal colour/pattern throughout the species' range. There is great variation in wing markings. This caused the morphs of *P. spumarius* to be given species status by many earlier authors. More than sixty synonyms have been given to the species due to its colour variation (2). In addition, some morphs have been given subspecies status (72). Numerous varietal names have been listed concerning the morph differences (44,73-75). Many different names have been given to the same colour forms. Consequently, these have caused confusion in the nomenclature. The meadow spittlebug was commonly called *Philaenus leucophtalmus* in the early literature. However, Ossiannilsson (76) stated that the name *P. spumarius* was consistent with the original intention of Linnaeus and the International Commission of Zoological Nomenclature in 1961 decided on the valid specific name as *spumarius* (77).

The dorsal colour/pattern variation of the meadow spittlebug has attracted many researchers in ecological and genetical studies. Classifications of the phenotypes have been made by several authors (29,31,34,61,77-80). The number of colour/pattern phenotypes has been the source of some debate (15,25, 30,74,81-83). Initially, nine phenotypes were determined, then, Stewart and Lees (10) suggested that there are thirteen main colour phenotypes. According to my extensive literature survey in the present paper, 16 phenotypes are found in many natural populations (Fig. 1).

Inheritance of eleven commonly occurring colour phenotypes has been studied extensively (41,70,71). These colour phenotypes are clearly inherited and are referred to by three-letter abbreviations for convenience, as follows: *populi* (POP), *typicus* (TYP), *trilineatus* (TRI), *marginellus* (MAR), *lateralis* (LAT), *flavicollis* (FLA),

gibbus (GIB), *leucocephalus* (LCE), *quadrimaculatus* (QUA), *albomaculatus* (ALB), and *leucophthalmus* (LOP). The first three are essentially very pale brown (golden) with darker mottling or stripes (the non-melanics) and the remaining are predominantly black or dark brown with pale markings in various combinations on the vertex, pronotum and wing patterns (the melanics). The other phenotypes: *vittatus* (VIT), *marginellus/flavicollis* (MAR/FLA), *ustulata* (UST), *praeusta* (PRA), and *hexamaculata* (HEX) rarely occur in different natural populations (10,26,30,39,73,81,83,84).

In some populations, certain phenotypes, particularly dorsal melanics are not expressed in males as clearly as in

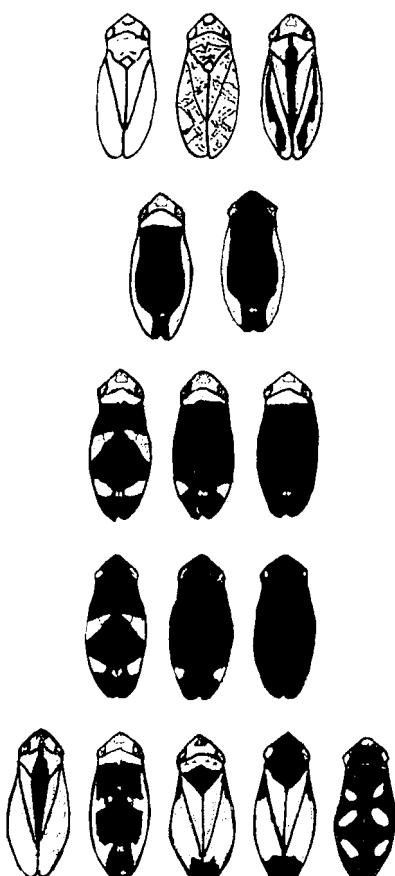


Figure 1. The 16 dorsal phenotypes of *Philaenus spumarius* occurring in many natural populations. The top row, the non-melanics, from left to right are: POP, TYP, TRI. The bottom row, the rare phenotypes are: VIT, MAR/FLA, PRA, UST, HEX. The remaining are melanics. The second row: MAR, LAT. The third row: FLA, GIB, LCE. The fourth row: QUA, ALB, LOP. Full names of the phenotypes are given in the text.

females, for example, in Finnish populations melanics seem to be limited to females (81). In British populations from south Wales there is no obvious differences between the sexes in overall melanic frequency (71). Large population samples from all over Turkey do not indicate any sex limitation, but significant phenotype variations occur between certain populations (Yurtsever and Zeybekoglu, unpublished data).

The genetic basis of the dorsal colour/pattern polymorphism

The dorsal colour/pattern polymorphism is determined by seven alleles at a single locus with complex dominance and co-dominance relationships (Fig. 2). Eleven principal phenotypes can be divided into groups as melanics and non-melanics (Fig. 1) (10). One of the three non-melanic phenotypes, TRI, is controlled by the allele 'T', the other non-melanics POP and TYP are controlled by the same allele 't'. The two main melanic groups (FLA) + (GIB) + (LCE) and (QUA) + (ALB) + (LOP) are controlled by one allele each at the main colour locus, the alleles 'C' and 'O' respectively (70, 71). Another non-melanic phenotype, VIT, is also thought to be controlled by the allele 'T' (10). On the other hand, there is another allele 'F' which is responsible for producing the FLA phenotype alone. Hence, the phenotype FLA is an expression either of the allele 'C' or 'F'. Moreover, two other melanics, MAR and LAT, are controlled by the alleles 'M' and 'L' respectively. Some of the white head/elytral patterns are co-dominant. For example, MAR can also be expressed in the heterozygote condition by the combinations of the alleles L/C and L/F (Fig. 1). The alleles producing white patterns in head/elytral margins are dominant over the alleles responsible for dark pigmentation in corresponding parts (9). Furthermore, there may be some other non-allelic loci or locus responsible for the regulation of the phenotypic variation within each group (85).

The genetic basis of the rare phenotypes mentioned before is not very clear. Thompson and Halkka (83) point out that the UST appears to be a variant within the populi-typica complex. VIT and PRA are often considered minor modifications of TRI (33,73,83), but Stewart and Lees (10) have regarded them separately from TRI and they suggested that VIT is variety of TRI. However, none of these authors presented inheritance data. Based the laboratory data, Yurtsever (67) proposed that VIT is a variety of TRI and suggested that HEX, PRA and UST are expressed by different alleles.

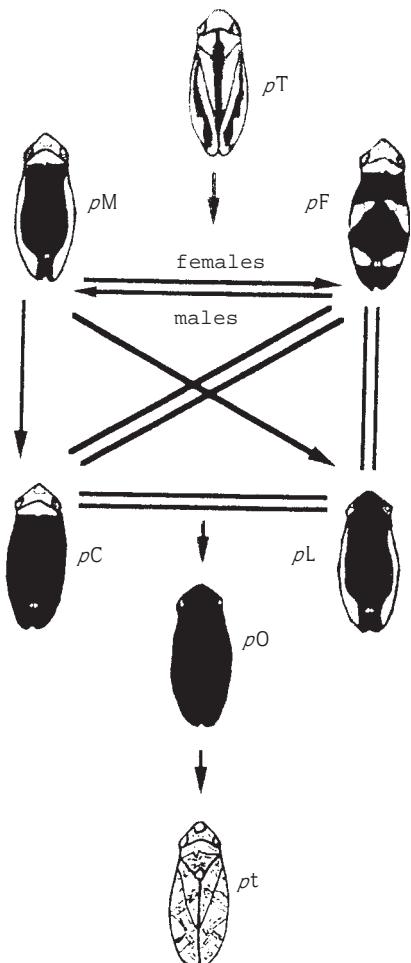


Figure 2. Dominance hierarchy for the 11 common phenotypes of *Philaenus spumarius* in some British populations. Arrows show direction of dominance and double lines show co-dominance. The p donates pigmentation locus "p" for seven alleles. Each phenotype in the figure represents its own phenotypic group as described in the text. (After Stewart and Lees 1996).

The dominance hierarchy models of common eleven phenotypes for the two regions, Fennoscandia and south Wales urban are well known. Halkka et al. (70) have demonstrated that the dominance relationships in Fennoscandian populations are different in the two sexes. Accordingly, in both sexes the allele TRI is top dominant but in males POP/TYP are dominant to the melanics whereas in females the melanics occupy the second place after the allele TRI, followed by POP/TYP in the hierarchy. However, Stewart and Lees (71) have found no different pattern of dominance in the two sexes, TRI is again top dominant followed by the melanics then POP/TYP are bottom recessive in males as well as in

females. They have also found reversal of dominance between the alleles MAR and FLA-F concerning the sexes. Their breeding experiments reveal that MAR is dominant over FLA-F in females, conversely MAR is recessive in males (Fig. 2). The dominance hierarchy between the phenotypic groups can be summarised as in Figure 2.

In New Zealand populations, only two phenotypes, FLA and TYP, occur (37) and FLA is dominant over TYP in both sexes (41). The model of inheritance in a rural Welsh (Llys dinam) population (67) is slightly different from two previous studies involving Fennoscandian and urban Welsh (Cynon Valley) populations. The Llys dinam model fundamentally follows the Cynon Valley model but differs in the inheritance of MAR. Because in the Llys dinam population, MAR is to be found dominant over TYP in females but recessive in males similar to the Finnish model, but the dominance hierarchy of the other phenotypes is the same as in the Cynon Valley model. The Llys dinam model is supported by the more restricted investigation of the Skokholm, west Wales (67) and Turkish populations (18). Although some authors suggested that FLA and LAT are co-dominant with each other (10,70), they presented no data confirming their reports. Nevertheless, Yurtsever (67) found clear experimental evidence supporting their suggestions.

Geographic variation of dorsal colour/pattern phenotypes

The occurrence and frequencies of the dorsal colour/pattern phenotypes vary from location to location. Several selective influences associated with the environmental factors have been suggested (26). Patterns of variation may be affected by the habitat composition (86). Variation in morph frequencies may even occur within one habitat at the subniche level is associated with the host plant types. Geographic variation in morph frequencies across Europe is parallel to changing climatic conditions (81,87). From North American populations eight phenotypes, whereas from Italian populations fifteen phenotypes have been recorded. Although *P. spumarius* has been recorded from several parts of Turkey (38,40), there is very limited information about morph variations (18,39).

The large scale geographic variation indicates that most melanics with some exceptions are increased in frequency from south to north in some American and European populations (82,88). The latitude is associated with morph frequency variation (26,28). Increasing

melanic frequencies are positively correlated with altitude (15,32). Accordingly, Thompson (82,88) proposed that the high melanic frequency association with the cooler climates is a consequence of thermal selection. Consistent with the hypothesis, Berry and Willmer (89) experimentally verified that thermal melanism is possible.

Studies on British populations have shown that industrial melanism occurs in *P. spumarius* (90). There is a strong association between the high melanic frequencies and intense atmospheric pollution in some urban areas where industrial pollution has occurred (91,92). In contrast, no association is found between melanic frequencies and degree of pollution in industrial areas in Chicago and Czechoslovakia (83,93), respectively. Although *P. spumarius* populations show industrial melanism, the selective mechanisms are not clearly known which are responsible for maintaining this polymorphism. The associations may be climatic with colour and pattern functioning as an important thermoregulatory component. However, the effects of predation and the other direct effects of air pollution cannot be ruled out (90).

The importance of the predation is also known in the polymorphism of *P. spumarius*, this is probably one of the selective forces influencing the polymorphism (42,94,95). Birds are presumably the most likely predators serving for apostatic selection (1,96). In addition to the deterministic influences discussed, the stochastic effects have also been shown in some island populations in the Finnish Baltic (85,97-99). These studies have demonstrated that low variability and morph frequency differentiation on the small isolated island populations were due to genetic drift. The presence of only two of the eleven phenotypes in New Zealand and Hawaii populations are consistent with loss of genetic variation due to the founder effect (9, 37).

The ventral colour/pattern variation

As with its dorsal colour/pattern polymorphism, the meadow spittlebug *P. spumarius*, exhibits remarkable variation on the ventral surface. Although there are records from East European, Russian (30,84), Finnish (100) and North American (88) populations dealing with ventral variation in *P. spumarius*, virtually no detailed work had been done until recently (67,101).

West (101) surveyed several populations of *P. spumarius* in England and Wales and found variation from very dark to light on the ventral surface. He analysed 18

characters of the ventral surface according to their darkness level. This revealed that the darkness on the ventral surface is associated with the dorsal phenotype. West (101) also demonstrated the influences of sex and location on ventral darkness. Detailed laboratory studies demonstrated that the ventral darkness of certain TRI phenotypes is associated with its genotype (67,101). That is, dark ventral TRIs are heterozygous for a dorsal melanic phenotype and light ventral TRIs are heterozygous for POP or TYP.

Svala and Halkka (100) have shown clinal variation in the patterning of the frontoclypeus in females from several Finnish populations and have suggested that the frons patterning differs between the sexes. Beregovoi (84) reports that the sexes show differentiation on the frons and pleurites with regard to pigmentation. His study reveals that the frequency of *P. spumarius* males with dark pleurites increases from south to north in Russian populations. In North America, a similar increased frequency of dark pleurites in males towards the north and cooler temperatures is found (88). Striking variation in the frontoclypeal patterning also occurs in several British populations (101).

Svala and Halkka (100) mentioned that pigmentation on the frontoclypeus is genetically determined, though they provided no evidence from crossing experiments supporting this assumption. West (101) suggests that ventral darkness in *P. spumarius* is discontinuous, and is under genetic control, and the same colour locus responsible for dorsal melanism possibly controls pigmentation on the ventral surface. Parallel to those suggestions, recent experimental evidence confirms that ventral darkness in *P. spumarius* is a heritable trait (67). Interestingly, certain British and Turkish populations show significant differences in the ventral darkness (67). This is probably due to different selection regimes that the populations are responding to.

Polyandrous aspect of *Philaenus spumarius*

This striking aspect of the meadow spittlebug was just recently reported (102). The female *P. spumarius* may copulate several times with different males during the reproductive period of the life span. Consequently, different males may father the offspring of the same female. Multiple mating does not influence the number of the progeny, but it may provide great genetic and thus evolutionary benefits to the meadow spittlebug as reported in many polyandrous species (103-106).

Discussion

The studies with *P. spumarius* reveal that the dorsal colour/pattern polymorphism occurs throughout its extensive range. These include small isolated island populations (97,99) and even localised populations in fine-grained environments as in the examples of the areas which are exposed to intense particulate air pollution the Cynon Valley (91) and the Cardiff Docks (92). Although the occurrence and frequency of the phenotypes vary in different environments (9,10,37,90) no populations have yet been found with a fixed allele.

The general applicability of the inheritance of dorsal colour/pattern polymorphism emerging from previous studies is supported with the material from rural populations of Britain, New Zealand, and Turkey. In addition to seven alleles of dorsal polymorphism, it appears that there may be another allele controlling the expression of the phenotypes UST (*ustulata*) and HEX (*hexamaculata*), but this is not conclusive at present. Halkka et al. (87) reported that there might be two other alleles, the 'V' and 'P' responsible for the VIT (*vittatus*) and PRA (*praeusta*) phenotypes respectively. However, there is no sign of an independent allele for VIT (67), and this phenotype appears to be a variety of TRI, in agreement with previous suggestions (10). The position of PRA in this polymorphism is still unclear.

Some of the subtle differences in the inheritance of the dorsal colour/pattern polymorphism in *P. spumarius* between the areas studied may be related to local conditions acting as a selective effect on this polymorphism. The melanic forms may be more resistant to the influences of the effects of particulate or gaseous pollution in the polluted areas (91). Accordingly, the local environmental influences may be important for certain phenotypes in a given area. Thus, these conditions may provide some advantages to them over other phenotypes resulting in fitness, such as more efficiently evading predators, finding a mate and food resources (91).

Natural selection probably exerts its influence in the form of climatic selection (97). The importance of apostatic selection responsible for the variety and maintenance of the dorsal colour pattern polymorphism is emphasised (68). Thompson (94) argues that the apostatic selection hypothesis does not explain evolution of geographic variation, and particularly clinal variation. Nevertheless the MAR phenotype occurs, at a higher

frequency than other melanic forms in certain parts of North America (83), and this is attributed to aposematic selection (94,107). According to Thompson (94), black and white pigmentation of the MAR phenotype (in females) represents an example of escape warning coloration, and the pattern of this phenotype mimics avian excrement. Therefore, experienced predators ignore MAR individuals because they remember previous frustrating attempts with this similar pattern that they have encountered. However, experimental evidence for this hypothesis is lacking.

Owen (108) represents examples of similar polymorphisms in *P. spumarius* and the land snail, *Limicolaria martensiana* that are exposed to similar pattern selection. The colour pattern of the shell in the snail *L. martensiana* is extremely variable and the species is locally very abundant, occurring in high densities. The four shell forms in coloration apparently resemble dorsal phenotypes of *P. spumarius* (TYP, TRI, MAR, POP). The relative frequencies of the four forms of *P. spumarius* in an alfalfa field in Michigan and of the forms of *L. martensia* in a eucalyptus plantation near Kampala are parallel to each other. Relative frequencies of the colour forms in these two species are determined by apostatic selection, because the forms concerned are apparently cryptic and may be at a selective advantage over the non-cryptic forms.

In some circumstances, morph frequencies in natural populations of *P. spumarius* may reflect stochastic events (85,97-99) despite the view that all genetic polymorphisms are maintained, and morph frequencies determined by natural selection (109).

The mode of inheritance of this polymorphism in this species is simply governed by a one-locus system as is often observed in many arthropod species concerning melanism. However, the role of the modifier genes in the polymorphism of *P. spumarius* must be borne in mind (110), because observed genetic differences between various populations of a polymorphic species may not be only for the primary genes for melanic patterns but for their modifiers as well. The role of modifiers affecting the expression of the colour locus in many natural populations is now well understood (111,112). The studies with *P. spumarius* show another way in which the genetic architecture of natural populations could be changed by modifiers.

The influence of selective factors in ventral darkness is unknown. The differential ventral darkness variation in the meadow spittlebugs between Turkey and Britain is striking (67). British *P. spumarius* populations do not manifest geographic pattern in certain ventral parts (101). However, in some natural populations, ventral surface may respond to selection as the dorsal surface in certain environments. Moreover, some kind of non-visual selection may influence phenotype frequencies (91,92,113.). Variation in the populations concerned on a large geographic scale may be evident (30,88) and differences can be expected between widely separated populations concerning this particular character (84,100).

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Multiple paternity is probably a novel aspect in *P. spumarius* and would repay future study. Although information is limited for the incidence of multiple mating in the wild, it does occur in natural populations (102). Since this homopteran insect shows very high habitat diversity (10), multiple mating is probably one of the leading reasons of the species occupying numerous terrestrial habitats in many regions of the world, because multiple mating provides many evolutionary advantages to polyandrous species through increased genetic variability and high fitness (104-106).

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