

# Genetic control of colour polymorphism in spittlebugs (*Philaenus spumarius*) differs between isolated populations

Alan J. A. Stewart\* and  
David R. Lees

Department of Zoology, University College,  
Cardiff CF1 1XL, U.K.

Species that have extensive geographic ranges but limited gene flow may have evolved different genetic backgrounds in widely separated populations. The spittlebug *Philaenus spumarius* is highly polymorphic for dorsal colour/pattern throughout its extensive northern temperate range. In Scandinavian populations, the eight melanic morphs are wholly or substantially restricted to the females and are dominant to typical in females but recessive in males. In a survey of 548 populations in England and Wales, the same morphs are regularly expressed amongst males and melanic frequencies in the two sexes approach equality, suggesting a different mode of genetic control. Laboratory breeding experiments using British stock demonstrate the dominance of melanics to typical in males as well as females. It is suggested that this difference in inheritance for the same polymorphic trait is due to different dominance modifiers in populations from the two regions.

## INTRODUCTION

It is generally accepted that the genetic control of a particular trait is uniform throughout a species' range. This assumption is usually justified and has often been confirmed by detailed experimentation. However, in species with restricted gene flow and geographic ranges which encompass large environmental gradients or transgress major physiographic barriers, the same traits could have a different genetic basis in allopatric populations if selection and adaptation differ sufficiently from one isolate to another.

The spittlebug *Philaenus spumarius* (L.) is a common and widespread insect which exhibits a wide ecological amplitude over most of the northern hemisphere. Being a weak and infrequent flier, its vagility, insofar as this has been measured (Halkka *et al.*, 1967a), is estimated to be very low. It is polymorphic for adult dorsal colour/pattern in all populations studied to date, which cover North America (Thompson, 1984), Europe (Halkka *et al.*, 1967b, 1974, 1975, 1976; Raatikainen, 1971) and Asia (Whittaker, 1972). The zoogeography of this species therefore suggests that it is a possible candidate for showing

such genetic divergence. Here, we report evidence from both field populations and laboratory breeding experiments which suggests that the genetic basis of melanism in this species has differentiated significantly between British and previously-studied Scandinavian populations. This paper is a summary of our findings; the details of geographic variation in morph frequencies, the breeding experiments and methodology will all be reported separately.

## THE COLOUR/PATTERN POLYMORPHISM

There are 11 principal and regularly-occurring colour morphs (Halkka *et al.*, 1973). For convenience we arrange the phenotypes into three groups. *Trilineatus* has three dark longitudinal stripes against a pale background; *typicus* has variable mid-brown mottling or cross-patterning on a pale background and is combined, for the purpose of this analysis, with the unicolorous pale sandy brown form *populi*. The remaining eight morphs constitute the melanic grouping, being predominantly black or dark brown with various arrangements of pale markings on the head and wing margins. Halkka *et al.* (1973) have demonstrated that the polymorphism is inherited at a

\* Present address: Department of Entomology, Rothamsted Experimental Station, Harpenden, Herts. AL5 2JQ, U.K.

single autosomal locus with seven alleles and various assumed unlinked modifiers.

## METHODS

All field samples were collected with a sweep net from a variety of herbaceous plants and habitat types. Samples were taken most frequently from thistles (primarily *Cirsium arvense* (L.) growing on disturbed or waste ground. Laboratory breeding experiments consisted of individual pairings between unmated stock, set up in cages containing dwarf broad bean plants (*Vicia faba* cv. "The Sutton"). Temperature and photoperiod were controlled to break the naturally occurring ovarian and egg diapauses and thereby to shorten the normal univoltine life cycle.

## RESULTS

### *Morph frequencies in field populations*

Present knowledge of the ecogenetics of this species is drawn mostly from studies in southern Scandinavia (Halkka, 1964; Halkka *et al.*, 1967*a*, *b*, 1976). The most striking feature of populations in that area is the strict female-limitation of four melanic phenotypes and the rare occurrence amongst males of the other four. As a consequence, total melanic frequencies are much lower in males than in females (table 1). By contrast, in a recently-completed survey of 548 populations in England and Wales, the melanic frequency amongst males is only slightly lower than that for females (table 1). The eight melanic phenotypes differ in penetrance in males. In British populations, morphs which were formerly regarded as strictly female-limited occur regularly in the males, although at lower frequencies than in females.

Frequencies of the other melanics are approximately equal between the sexes. Total melanic frequencies in the two sexes are not significantly different in most populations throughout England and Wales. The most striking demonstration of this is found in populations close to a source of intense localised air pollution in the Cynon Valley (S. Wales), which has exceptionally high melanic frequencies (Lees and Dent, 1983) and shows the greatest penetrance of melanic phenotypes in males.

### *Breeding experiments*

On the basis of evidence from a much smaller number of populations, it was previously suggested that these differences between British and Scandinavian populations in terms of the penetrance of melanic genes in males might reflect important differences in underlying genetic control (Lees *et al.*, 1983). This possibility has now been investigated through detailed breeding experiments using material from the Cynon Valley.

Results from breeding experiments using material from populations in S. Finland (Halkka *et al.*, 1973) are presented for comparison with our data (table 2). In Scandinavian *Philaenus*, crosses between melanic females and pure-bred *typicus* males produce a 1 melanic:1 *typicus* segregation in the female offspring but only *typicus* amongst males (table 2(i)). These and other results suggest that melanics in these populations are dominant to *typicus* in females but recessive in males.

In our experiments with British stock, the combined progeny from reciprocal crosses between melanic and *typicus* parents show good approximations to 1 melanic:1 *typicus* segregations in both sexes (table 2(ii) and (iii)). Several replicates of this cross type produced only melanic offspring (table 2(iv)). Intercrosses between melanic parents

Table 1 *P. spumarius* morph frequency data for populations in S. Finland and Britain

Geographic area	No. of pops	<i>trilineatus</i>	melanics	<i>typicus</i>	Total	Per cent melanic	CPR†
S. Finland*	60	♂ 456	78	14,975	15,509	0.50	0.028
		♀ 482	2945	12,790	16,217	18.16	
Cynon Valley	36	♂ 900	5213	3,370	9,483	54.97	0.954
		♀ 732	4400	2,509	7,641	57.58	
Britain (excl. C.V.)	512	♂ 9117	5235	33,847	48,199	10.86	0.699
		♀ 7263	5997	25,309	38,569	15.55	

\* Combined data from Halkka (1962; 1964, data for S.W. Finland only), Halkka *et al.* (1970) and Boucelham and Raatikainen (1984).

† Cross-product-ratio (CPR) calculated as (melanic ♂♂/total ♂♂) (total ♀♀/melanic ♀♀) where totals exclude *trilineatus* contribution. CPR scale ranges from 0 (no male melanics) to 1 (melanic frequencies equal in males and females).

**Table 2** Results of *Philaenus* breeding experiments, using material taken from populations in Scandinavia (Halkka *et al.*, 1973) and Britain (present study)

Cross type (♂ × ♀)	No. of families	Progeny				Total	G-tests	
		♂	melanic ♀	♂	typicus ♀		G of F*	2 × 2†
<b>Scandinavian material</b>								
(i) <i>typicus</i> × melanic	22	—	189	344	173	706	0.71‡	NA
<b>British material</b>								
(ii) <i>typicus</i> × melanic	6	33	23	35	37	128	2.01‡	1.35
(iii) melanic × <i>typicus</i>	11	34	34	42	36	146	0.69‡	0.22
(iv) melanic × <i>typicus</i> ¶	10	27	33	0	0	60	NA	NA
(v) melanic × melanic	10	39	41	14	9	103	0.40§	1.06
(vi) <i>typicus</i> × <i>typicus</i>	6	0	0	39	27	66	NA	NA

\* Goodness-of-fit *G* tests against expected segregations.

† 2 × 2 contingency table *G*-tests of association between colour morph and sex.

‡ 1 melanic: 1 *typicus*.

§ 3 melanic: 1 *typicus*.

|| Only females tested.

All tests: *df* = 1; NA, not appropriate; All departures from expectation not significant (*P* > 0.2).

¶ Families where progeny did not segregate between melanic and *typicus*.

taken from the segregating families produced good agreement with a ratio of 3 melanic: 1 *typicus*, again in both sexes (table 2(v)). Intercrosses between *typicus* parents produced only *typicus* offspring (table 2(vi)). Some of the males amongst the latter progeny were relatively dark but nevertheless readily distinguishable from melanics; none of the female progeny from these crosses presented any scoring difficulties.

## DISCUSSION

Results of the breeding experiments demonstrate that melanics in British *Philaenus* populations are dominant to *typicus* in both sexes, in marked contrast to the mode of inheritance in Scandinavian populations where this applies in females but not in males. Our results do not conflict with those from previous experiments in Finland. In both studies, the conclusions from breeding experiments are supported wholly by morph frequencies in the field populations from which the breeding material was taken. In fact, we suggest that a comparison of melanic frequencies between the sexes will indicate the underlying genetic control in any particular population.

Early experiments with poultry (Fisher, 1935) and moths (Ford, 1940) indicate that dominance at one locus is affected by genes at separate loci. These dominance modifiers may vary geographically so that outcrossing to populations where the appropriate modifiers are either different (Ford,

1955) or absent (Kettlewell, 1965) will produce a breakdown in dominance. Examples of dominance breakdown or reversal have also been recorded in mimetic butterfly polymorphisms (Clarke and Sheppard, 1960; Clarke *et al.*, 1985; Sheppard *et al.*, 1985), but these usually involve disruption of the genetic background through crossing individuals from different populations. By contrast, melanism in *Philaenus* appears to be a unique case of the direction of dominance in one sex being reversed in different and independently-studied populations. We suggest that the "genetic architecture" of the polymorphism in the two regions has evolved differently, probably through the development of differences at loci modifying the colour/pattern locus.

The existence of two modes of inheritance for the same array of visible polymorphic variation invites speculation on the selective advantage of such differentiation and the nature and location of the boundary between the two types. So far, our experiments have used material only from the Cynon Valley or nearby populations in south Wales, where selection for melanism is undoubtedly strongest. We have yet to test whether the same model of inheritance applies to other areas of Britain, although an examination of morph-frequencies in field populations suggests that it probably does in most populations. Given the differences between our results and those from previous studies (Halkka *et al.*, 1973), the other obvious approach, which we are now adopting, is to observe dominance when Scandinavian and British *Philaenus* are intercrossed.

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