GEOGRAPHICAL, SPATIAL AND TEMPORAL VARIABILITY IN THE BALANCED POLYMORPHISM OF *PHILÆNUS* *SPUMARIUS*

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1. INTRODUCTION

THE meadow spittlebug, *Philænus spumarius* L. (Homoptera), is found from the British Isles to Japan, from Sicily to Lapland and everywhere in North America from California to Canada. In many places along its range the species is also very abundant, reaching population densities of more than 400/m² in alfalfa (lucerne or *Medicago sativa*) fields in the United States. Especially in the U.S.A. and Canada, but also in some parts of Europe, *Philænus* is a serious pest of cultivated Leguminosæ and Graminaceæ, and for this reason its biology and ecology have been studied fairly intensively (Weaver and King, 1954).

Many of the spittle insects (family Cercopidæ) are polymorphic, but none is known to possess such a long series of colour forms as *P. spumarius*. Unfortunately, these forms, often called "varieties", are given different names by different authorities. Many of the forms occur in the females only, but none is confined to the male sex. In Central Europe, 14 or more different forms are encountered in the females, in Finland 12, and the American workers report the occurrence of only eight forms. Most of the forms are very distinct and easy to recognise, but intergrades occur between some of them. In fig. 1, 14 different types of pattern are represented, together with one form combining two of the 14 commonly occurring phenotypes. As shown below, specimens coloured like the one shown in lower right corner of fig. 1 are very rare. However, as pointed out by Wagner (1955), their presence shows that the different phenotypes of *Philænus* are produced by the interaction of pigment-forming factors with slight site-specificity and pigment-inhibiting factors with strict site-specificity.

For classification purposes, the completely dark form *lop* (*leuco-phthalma*) may thus be chosen as the basic morph. On the upperside of the insect, there are seven distinct fields which may appear unpigmented, as indicated in fig. 2. The fields marked *f*₁-*f*₄ constitute one series of phenovariation, and fields marked *v*₁-*v*₂ are seldom unpigmented simultaneously with the *f* fields. On the other hand, the *c* field (cephalo-pronotal) combines freely with all the combinations of the *f* series as well as with those of the *v* series. In all the forms the overall intensity of pigmentation is variable, from medium brown to black, and irrespective of the intensity, tiny white spots amidst pigmented areas are possible.

FIG. 1.—The colour forms of *Philenus spumarius*. The forms *populi* (POP), *typica* (TYP), *trilineata* (TRI), *marginella* (MAR), *lateralis* (LAT), *flavicollis* (FLA), *gibba* (GIB), *leucocephala* (LCE), *quadrinaculata* (QUA), *albomaculata* (ALB), *leucophthalma* (LOP) and *præusta* (PRA) are found in Finland. The forms *vittata* (VIT) and *ustulata* (UST) occur in Central Europe. The form LAT+QUA is a very rare combination of two common phenotypes.

FIG. 2.—The fields which may appear unpigmented in *Philenus*. Fields belonging to the *v* (*vittata*) series seldom occur together with fields belonging to the *f* (*fasciata*) series. The *c* (*cephalo-pronotal*) field combines freely with all the other combinations. With the help of this system, nine of the phenotypes can be expressed as follows:

tri	$v_1 + v_2$	fla	$c + f_1 + f_2$	qua	$f_1 + f_2$
mar	$c + v_1$	gib	$c + f_2$	alb	f_2
lat	v_1	lce	c	lop	o

Since it may be of some general interest to ascertain how such a long series of forms responds to different environmental conditions, a quantitative study was begun by the author in 1956 and continued during the years 1960-63. Most of the results which emerged from this study only parallel those obtained in the pioneering work on snails,

FIG. 3.—The sites of collecting. Aland region: Separated from a bunch of collecting sites lie Aero (A) and Ulkosaari (U). SWF region: Bromarv (B), Tvärminne (T), the two Nurmijärvi populations (N) and Pälkäne (P). NEF region: Oulujärvi (O), Ylämaa (Y), Kuusamo (K) and Määttälä (M).

butterflies, coleopterans, fruit flies, etc., but the peculiar habits of *Philænus* also introduce some unusual features into a discussion of the factors involved in this special case of polymorphism.

2. MATERIAL AND METHODS

Samples have been taken from 20 populations in Finland. From two of the populations, data are available from 1956 and from the four successive years 1960-63. From five additional populations, samples have been collected during at least two summers, the remaining 13 populations having been visited during 1963 only. The total material now consists of 50,010 specimens, of which 26,788 are males and 23,222 females. The localities of collecting are given in the accompanying maps (figs. 3 and 4). The southernmost population, Tvärminne (T_A), lies at 59° 51', the northernmost one, at 66° 05', being Määttälä (M), only 50 kilometres south of the Arctic Circle. The direct distance between the two most peripheral populations, Eckerö (E) and Määttälä, is about 820 km. or 510 miles.

Sampling was done with a sweep net on hay fields from which the hay had recently been removed, the fields being covered with stubble and some secondary growth. Precautions to minimise sampling errors, as given by Halkka (1962b), were practised. The most serious source of error is the possible presence of a "Howanitz (1953) effect", since the array of forms includes both very light and very dark morphs. These may, under intense sun radiation, choose different positions on the stems. Although it has not been possible to sample all the 20 populations under similar conditions, attempts were made to sample in fine weather and between 10 a.m. till 2 p.m.

The plant communities of the fields were variable, with 10-40 common species per hectare on all the collecting sites. The dominant plants (*Phleum* and *Trifolium*) were, for the most part, the same, however.

3. OBSERVATIONS

(i) *Geographical: the three regions*

The 20 populations have been divided into three regional groups. Firstly, the Åland region contains populations from Eckerö, Geta, Finström, Hammarland, Saltvik, Raunio, Jomala, Lemland, Viiniö, Aero and Ulkosaari. Secondly, the SWF (South Western Finland) region contains Bromarv, Tvärminne, the two Nurmijärvi populations and Pälkäne. Thirdly, the NEF (North Eastern Finland) region contains Oulujärvi, Ylämaa, Kuusamo and Määttälä.

Using the 1963 data, a comparison was made between the Åland, SWF and NEF regions. Altogether, 28,547 specimens were collected, 15,147 of them males and 13,400 females. Since the full array of colour variation is displayed by the females only, the results are given for this sex first (table 1).

The table shows very clearly that the frequency of *pop* is much higher in Åland than in SWF or NEF. In fact, even the specimens from Åland, assigned to *typ* in the table, are on the average far lighter than the *typ* from SWF or NEF. Moreover, in Åland *typ* is more heterogeneous than on the mainland and contains brownish pigmented forms with irregular patterns.

In Åland *tri* is far less frequent than in SWF, and in the NEF region some populations (O and K) show relatively high *tri* frequencies.

Certain of the Åland populations, especially the four easternmost ones (L, V, A and U), have extremely low proportions of *tri* and it is quite possible that V and U lack this form completely.

FIG. 4.—The Åland region. Populations: Eckerö (E), Geta (G), Finström (F), Hammarland (H), Saltvik (S), Raunio (R), Jomala (J), Lemland (L), Viinö (V), Aero (A) and Ulkosaari (U).

All the Åland populations, compared with the SWF and NEF populations, are low in *mar* and *lat*, relatively high in *fla* and very low in *gib* and *lce*. It is possible that the isolated island population U lacks

mar and *lat* completely and is thus devoid of all the pigment-inhibiting factors belonging to the *v* series.

The frequencies of the *qua* and *alb* forms are variable and no trends are observable within the Åland region, but *lop*, the entirely dark form, seems to be slightly rarer in the east than in the west. The presence of *pra* in all the populations of the main island of Åland (its absence in the small H sample is fortuitous) and its absence in the eastern island

TABLE 1
Composition of the 19 populations sampled in 1963. The females

Population	<i>pop</i>	<i>typ</i>	<i>tri</i>	<i>mar</i>	<i>lat</i>	<i>fla</i>	<i>gib</i>	<i>lce</i>	<i>qua</i>	<i>alb</i>	<i>lop</i>	<i>pra</i>	Total
Eckerö .	32	204	2	2	2	8	1	1	2	—	3	2	259
Geta .	62	185	2	3	1	5	—	1	6	2	4	3	274
Finström .	34	168	—	—	—	6	—	2	4	1	—	3	218
Hammarland	21	48	1	2	1	1	—	—	—	1	1	—	76
Saltvik .	43	194	—	1	2	12	1	3	4	2	4	3	269
Raunio .	202	849	7	14	21	30	5	3	25	21	19	16	1212
Jomala .	50	309	3	3	4	8	2	2	2	—	8	6	397
Lemland .	123	618	1	5	36	23	—	1	9	4	15	6	841
Viinö .	112	1223	—	10	33	56	5	2	23	13	3	5	1485
Aero .	78	888	1	8	10	36	2	2	17	1	6	—	1049
Ulkosaari .	61	570	—	—	—	6	1	5	7	—	2	—	652
Bromarv .	22	738	10	74	28	20	11	6	14	4	4	—	931
Tvärminne .	11	565	22	36	45	10	11	12	2	9	7	—	750
Nurmijärvi A	20	855	45	56	71	17	8	13	7	20	18	—	1132
Pälkäne .	—	197	8	12	17	4	3	4	—	3	5	—	253
Oulujärvi .	2	547	36	31	44	17	7	15	5	13	34	—	750
Ylämaa .	19	252	7	4	17	3	7	3	3	7	8	—	330
Kuusamo .	13	1264	179	33	79	98	43	77	42	163	156	—	2145
Määttäälä .	3	221	5	5	30	15	12	29	5	24	28	—	377
Sum total . . .													13,400

populations A and U obviously mark the north-eastern limit of this form. On the Finnish mainland this form has never been found, but in Sweden it does occur.

Differences between populations of the SWF and NEF regions are less remarkable than between Åland and the other two. However, in at least two north-eastern populations *tri* is distinctly more frequent than in any of the SWF populations. All the dark forms are distinctly commoner in NEF than in SWF and reach quite high frequencies in the two northernmost populations, K and M.

In table 2, the 1963 male samples are given from the 19 populations visited during that year. The absence of the *mar*, *lat* and *pra* columns shows that these forms do not occur in the male sex. Furthermore, only in the NEF region were *fla* males found, and the forms *gib* and *lce* are entirely confined to the population M, close to the Arctic Circle. The

presence of these forms in the north is explainable on the basis of the generally heavy pigmentation of the NEF specimens. The high frequencies of *qua*, *alb* and *lop* in the NEF populations are in striking contrast to the almost complete absence of these forms in south-western continental Finland.

In Åland, dark forms are more frequent than in SWF, the R population showing especially high frequencies of all three forms. Concerning the light forms, the data presented in table 2 are to a large

TABLE 2
Composition of the 19 populations sampled in 1963. The males

Population	<i>pop</i>	<i>typ</i>	<i>tri</i>	<i>fla</i>	<i>gib</i>	<i>lce</i>	<i>qua</i>	<i>alb</i>	<i>lop</i>	Total
Eckerö	81	130	7	—	—	—	3	1	—	224
Geta	110	192	1	—	—	—	1	3	2	309
Finström	82	170	—	—	—	—	3	—	3	258
Hammarland	35	47	—	—	—	—	2	—	1	85
Saltvik	79	209	1	—	—	—	3	2	5	299
Raunio	418	971	7	—	—	—	20	16	25	1457
Jomala	129	397	2	—	—	—	4	5	7	544
Lemland	393	630	1	—	—	—	2	8	9	1043
Viinö	468	911	—	—	—	—	7	7	5	1398
Aero	143	982	1	—	—	—	4	5	8	1143
Ulkosaari	45	709	—	—	—	—	5	11	5	775
Bromarv	17	850	11	—	—	—	3	1	—	882
Tvärminne	33	883	28	—	—	—	—	—	—	944
Nurmijärvi A	—	998	38	—	—	—	9	—	—	1045
Pälkäne	—	198	8	—	—	—	—	—	—	206
Oulujärvi	—	793	57	6	—	—	13	13	4	886
Ylämaa	15	294	19	—	—	—	2	6	1	337
Kuusamo	4	2250	227	1	—	—	182	127	62	2853
Määttälä	—	366	14	8	1	2	41	14	13	459
Sum total										15,147

extent parallel with the corresponding values for females given in table 1. The uniformly yellowish *pop* is again very clearly most frequent in the Åland region. As with females, *tri* is rare in Åland and probably absent in certain populations. In NEF this form is abundant in the same populations which show high frequencies in table 1.

To gain a more general view of the differences between Åland, SWF and NEF, the colour form frequencies from the separate populations within each region were pooled. The sums so obtained, together with the respective percentages, are seen in table 3. In both sexes, Åland is characterised by high *pop*, low *tri*, and moderate *qua*, *alb* and *lop* frequencies, as compared with SWF. In the female sex, Åland is higher in *fla* and lower in *mar*, *lat*, *gib* and *lce* than SWF. As compared with SWF, NEF is high in *tri*, *qua*, *alb* and *lop*, also in *lce* and the other dark forms with white head and pronotum.

For a closer quantitative analysis, the chi square method was applied for the differences between the three regions in the colour form frequencies. Only the females were taken into account and the following results were obtained:

Aland with SWF $\chi^2 = 3291.5$ d.f. 11 $P < 0.001$

Aland with NEF $\chi^2 = 1601.9$ d.f. 11 $P < 0.001$

SWF with NEF $\chi^2 = 445.0$ d.f. 10 $P < 0.001$

Statistically, Aland thus differs more from SWF than from NEF, and the two continental population groups differ far less from each other than from the Aland group of populations.

TABLE 3

Composition, in 1963, of the three regions. The absolute and relative (per cent.) frequencies of the colour forms are given

Region	pop	typ	tri	mar	lat	fla	gib	lce	qua	alb	lop	pra	summa
Aland $\left\{ \begin{array}{l} \text{♂♂} \\ \text{♀♀} \end{array} \right.$	1983 26.3	5348 71.0	20 0.3	— —	— —	— —	— —	— —	54 0.7	57 0.8	73 1.0	— —	7535
	818 12.2	5255 78.1	17 0.3	48 0.7	110 1.6	193 2.9	17 0.3	22 0.3	98 1.5	45 0.7	65 1.0	44 0.7	6732
SWF $\left\{ \begin{array}{l} \text{♂♂} \\ \text{♀♀} \end{array} \right.$	50 1.6	2929 95.2	85 2.8	— —	— —	— —	— —	— —	12 0.4	1 0.0	— —	— —	3077
	53 1.7	2375 77.5	85 2.8	178 5.8	161 5.3	53 1.7	33 1.1	35 1.1	23 0.8	36 1.2	34 1.1	— —	3066
NEF $\left\{ \begin{array}{l} \text{♂♂} \\ \text{♀♀} \end{array} \right.$	19 0.4	3793 81.7	317 7.0	— —	— —	15 0.3	1 0.0	2 0.0	238 5.3	160 3.5	80 1.8	— —	4535
	37 1.0	2284 63.4	227 6.3	73 2.0	168 4.7	133 3.7	68 1.9	124 3.4	55 1.5	207 5.8	226 6.3	— —	3602

To reveal whether the spittlebugs of the three regions differ in respects other than colour form frequencies, weighing experiments were made. Male specimens kept in dry storage for at least 3 months were weighed on a Mettler analytical balance. For weighing, the *typica* specimens of six populations of 1962 and of eleven populations of 1963 were chosen. The smallest number of specimens weighed was 366 (from Määttälä; see table 2), the highest number 2250 (from Kuusamo).

In both years the NEF specimens were about 20 per cent. lighter than the SWF or Aland specimens. The fact that the Jomala (J) specimens were relatively much lighter in 1963 than in 1962 may be attributable to overcrowding of this population in 1963. In 1963, the farmers were growing onions on the fields where hay was cultivated in 1962, and since for the *Philenus* population only ditches and roadsides were available as habitats, these were extremely heavily populated.

The northernmost populations thus seem to be characterised by a lower biomass production, since population densities in the NEF region are obviously not higher than in Åland or SWF. It may be noted in this connection that many of the Åland populations, especially Aero and Ulkosaari, were peculiar with regard to the large amount of fat given off by the animals after death. This high fat content perhaps has the function of protecting the insects against drought, a common calamity in Åland during the months of June and July.

As will be described in more detail below, in 1962 three samples were taken in Nurmijärvi A, one in July, one in early and one in late August. These samples are practically identical in the mean weight

TABLE 4

Mean weights of male typica specimens in two successive years. The specimens of 1962 have been kept in dry storage for 15 months, the specimens of 1963 for 3 months

Population	Mean weight 1962	Population	Mean weight 1963
Kuusamo	0.00240	Määttälä	0.00344
Nurmijärvi B	0.00263	Kuusamo	0.00356
Pälkäne A	0.00279	Oulujärvi	0.00419
Tvärminne A	0.00282	Jomala	0.00422
Nurmijärvi A—I	0.00286	Viiniö	0.00441
Nurmijärvi A—II	0.00304	Raunio	0.00443
Nurmijärvi A—III	0.00293	Ulkosaari	0.00447
Jomala	0.00307	Nurmijärvi A	0.00447
		Tvärminne A	0.00449
		Lemland	0.00452
		Aero	0.00473

of the male *typica* specimens (I, II and III in table 4). The weight of the males thus remained constant throughout the season.

In the light of the results presented above, both with regard to variation in colour pattern and variability in weight, there are great and statistically significant differences between the *Philænus* populations belonging to different regions. Against this dissimilarity between regions, differences between populations belonging to the same region but living scores of kilometres apart, may be contrasted. With consideration of only the varieties of the *v* series, such comparisons between the populations of SWF, namely T_A, the N populations and P, were performed by Halkka (1962*a* and *b*). Some of the χ^2 values obtained, which were significant in 1960, were not significant in 1961 and vice versa. The populations seem to fluctuate within certain limits and when two of them oscillate towards opposite ends of the range, significant values are obtained within the *v* series.

In the present paper, yearly variability is treated in a separate section. For the purpose of obtaining suitable values for comparison between some of the SWF populations in 1960-63, the annual

variability was reduced by pooling the frequencies of the separate forms from different years. For the years 1960-63, a χ^2 calculation between T_A and P_A , the two most distant SWF populations, yielded the value $\chi^2 = 54.6$, 10 d.f., $P < 0.001$. The respective values for the T_A-N_A and N_A-P_A comparisons were $\chi^2 = 31.1$ and 19.9, the P 's being less than 0.001 and a little less than 0.05.

The situation is somewhat different if the populations belonging to the Aland region are compared with each other. Owing to effective isolation, between R and A, for instance, the χ^2 reaches in the year 1963 a value of 100.0 (11 d.f.). Although the frequent intergrades between *pop* and *typ* render comparisons between populations belonging to the Aland region unsatisfactory, differences in the proportions of the easily recognisable forms are great enough to lead to very high χ^2 values.

As might be expected, yet higher χ^2 values are obtained, if two populations belonging to different regions are compared with each other. Thus, the χ^2 values for the $J-N_A$ and N_A-K comparisons, the 1962-63 frequencies being pooled, were 274.8 and 323.5, respectively.

In all the statistical calculations presented above, as well as in those that follow, only the females have been taken into account. This practice has been followed because only in the female sex do many of the colour forms appear distinct and easy to recognise.

(ii) *Spatial: differences between neighbouring populations*

Among the 20 populations, N_A and N_B in the SWF region are separated by a distance of only 1.6 km. (one mile) and S and R in Aland are separated by 2.3 km. Both between N_A and N_B and between S and R there lie considerable stretches of terrain uninhabited by *Philenus*.

Populations N_A and N_B were sampled in 1960, 1961 and 1962, but in 1963 it was no longer possible to take a sample at N_B because the land had been tilled and instead of hay, cereals were being grown on the plot. During 1960-62 the N_B field, on swampy ground, changed towards a wetter character, with plants such as *Juncus* gaining ground. This change was accompanied by a fall in the density of *Philenus*. The population at N_A lived on drier ground and did not show any change in density in 1960-62. In 1963 this field was also tilled but it was possible to take a sample at another plot about 100 metres from the original plot and separated from it by a narrow (20 metre) strip of trees and bushes.

The N_A and N_B populations were compared by a χ^2 analysis, the 1960-62 colour form frequencies of each population being pooled. The value obtained was $\chi^2 = 17.0$, with 10 d.f. and a probability P of 0.10-0.05, showing that the difference between the populations closely approaches formal statistical significance. Table 5, which includes the pooled frequencies as well as the theoretical (expected) frequencies

based on the null hypothesis, shows the differences to be due, in the main, to dissimilarities in the *mar*, *lce*, *fla* and *alb* frequencies.

In the 1963 sample at N_A , taken from a plot not effectively separated from the 1960-62 plot, the proportions of the different forms are practically identical with those of the earlier samples. A χ^2 analysis with the samples of the earlier years does not lead to significant values (see below, section (iii)).

Between the Saltvik (S) and Raunio (R) populations, the dissimilarity of the sample sizes and particularly the smallness of the S sample render comparison unsatisfactory. However, a χ^2 was calculated, $\chi^2 = 13.5$, corresponding to a P of 0.20.

TABLE 5

Observed and expected frequencies in two pairs of neighbouring populations

Population	<i>pop</i>	<i>typ</i>	<i>tri</i>	<i>mar</i>	<i>lat</i>	<i>fla</i>	<i>gib</i>	<i>lce</i>	<i>qua</i>	<i>alb</i>	<i>lop</i>	<i>pra</i>	summa
Nurmijärvi A 1960-61-62	14 15.8	1633 1619.4	84 83.4	88 105.6	124 121.4	35 29.7	33 33.8	39 33.8	6 9.9	24 27.4	43 42.6	— —	2123
Nurmijärvi B 1960-61-62	13 11.2	1142 1155.6	59 59.6	93 75.4	84 86.6	16 21.2	25 24.1	19 24.1	11 7.1	23 19.6	30 30.4	— —	1515
Saltvik 1963	43 44.5	194 189.4	0 1.3	1 2.7	2 4.2	12 7.6	1 1.1	3 1.1	4 5.3	2 4.2	4 4.2	3 3.5	269
Raunio 1963	202 200.5	849 853.6	7 5.7	14 12.3	21 18.8	30 34.4	5 4.9	3 4.9	25 23.7	21 18.8	19 18.8	16 15.5	1212

Both between N_A and N_B and between S and R, differences in colour form frequencies are thus nearly significant but smaller than are differences between populations belonging to the same region but separated by scores of kilometres.

(iii) *Temporal: the different years and different seasons of the summer*

It has been shown earlier (Halkka, 1962*a* and *b*) that from 1960 to 1961 the populations T_A , N_A , N_B and P_A remained constant. To see if any long-term trends occur, a comparison for the differences between 1960 and 1963, with the χ^2 method was performed for T_A , N_A and P_A , and for differences between 1952 and 1963 for the northernmost population M. The 1952 sample at Määttäälä was taken by Professor P. Kontkanen for synecological studies and later kindly given to me for colour form frequency analysis. It contains 1098 specimens, 587 of which are females.

The respective χ^2 values, with 10 degrees of freedom, were (T_A) 16.3, (N_A) 14.7, (P_A) 11.0 and (M) 8.7. The significance limit $P = 0.10$ lies at 16.0. Thus none of the values reaches formal significance but

at least two of them are suggestive of a slight change. However, from table 6 it is difficult to see whether there is any prevailing trend during these years.

TABLE 6

Observed and expected frequencies in samples taken, with 3 or 11 years intervening, from four populations

	pop	typ	tri	mar	lat	fla	gib	lce	qua	alb	lop	summa
Tvärminne 1960 .	7	446	19	13	33	6	2	3	—	4	9	542
Tvärminne 1963 .	7.6 11 10.4	432.5 585 598.5	17.2 22 23.8	20.6 36 28.4	32.7 45 45.3	6.7 10 9.3	5.5 11 7.5	6.3 12 8.7	0.8 2 1.2	5.5 9 7.5	6.7 7 9.3	750
Nurmijärvi A 1960 .	6	389	29	22	23	7	10	9	—	6	10	511
Nurmijärvi A 1963 .	8.1 20 17.9	386.9 855 858.1	23.0 45 50.1	24.9 58 55.1	29.2 71 64.8	7.5 17 16.5	5.6 8 12.4	6.8 13 15.2	2.2 7 4.8	8.1 20 17.9	8.7 18 19.3	1132
Pälkäne 1960 .	5	406	16	19	39	5	4	5	10	3	6	518
Pälkäne 1963 .	3.4 — 1.6	405.1 197 197.9	16.1 8 7.9	20.8 12 10.2	37.6 17 18.4	6.0 4 3.0	4.7 3 2.3	6.0 4 3.0	6.7 — 3.3	4.0 3 2.0	7.4 5 3.6	253
Määtälä 1952 .	5	335	11	20	33	25	16	42	8	18	74	587
Määtälä 1963 .	4.9 3 3.1	338.6 221 217.4	9.7 5 6.3	15.2 5 9.8	38.4 30 24.6	24.4 15 15.6	17.0 12 11.0	43.2 29 27.7	7.9 5 5.1	25.6 24 16.4	62.1 28 39.9	377

To gain an idea of selective forces acting on adult specimens during the season between their emergence and copulation, samples were taken at N_A in the years 1961 and 1962 at the beginning and end of the season. In 1961 the actual dates were 19 July for sample I and

TABLE 7

Observed and expected frequencies in samples taken in the summers 1961 and 1962, with 2 or 4 weeks intervening, from the N_A population

N_A	pop	typ	tri	mar	lat	fla	gib	lce	qua	alb	lop	summa
61/I .	5	522	26	35	50	11	9	14	2	12	17	703
61/II .	7.7 10 7.3	520.6 494 495.4	29.7 32 28.3	36.9 37 35.1	51.2 50 48.8	11.3 11 10.7	6.7 4 6.3	12.8 11 12.2	2.6 3 2.4	9.2 6 8.8	14.3 11 13.7	669
62/I .	3	722	29	31	51	17	14	16	4	6	16	909
62/III .	3.0 2 2.0	718.4 492 495.6	36.1 32 24.9	36.1 30 24.9	47.9 30 33.1	17.8 13 12.2	10.6 4 7.3	14.2 8 9.8	2.4 0 1.6	8.3 8 5.7	14.2 8 9.8	627

1 August for sample II, in 1962 24 July for sample I, 6 August for sample II and 22 August for sample III. The χ^2 values were:

between I and II of 1961: 8.1 10 d.f. P about 0.60

between I and III of 1962: 13.9 10 d.f. P about 0.20

The insignificance of these values shows that there is no strong selection operating during the season, such as would change the character of the form array completely. From table 7, a slight change in favour of *trilineata* is observable.

4. DISCUSSION

(i) Ecology of the species and maintenance of polymorphism

The ecology of *Philænus spumarius* has been studied by many authors, particularly in the U.S.A. and Canada. Ahmed and Davidson (1950) found that in Ohio the larval period lasts from about 10 April to 24 May, and thereafter the adults live through the whole summer, the females not depositing their eggs until September or October. In Finland, the first adults do not usually appear until the very beginning of July, and egg-laying begins in late August. In northern Finland the tempo of development is without doubt still faster.

Philænus is a univoltine insect (Wagner, 1955), and this is probably true of the insect throughout its range. According to King (1958), the number of adult specimens is highest soon after the relatively short hatching period and then declines. Cutting of the forage crops diminishes local spittlebug densities and disseminates populations over large areas. Evans and Lanham (1960) observed that specimens of *Philænus* migrating into fields distorted the pyramid of numbers in an insect community.

Many authors have noted the polyphagous nature of this insect and Gulijeva (1961) has listed some 80 species of plants as food resources of the meadow spittlebug in Azerbaidzhan. She notes that cereals, Compositæ, legumes and Labiatae are preferred to other plants. In Finland, *Philænus* populations are seldom dense on fields with underground drainage and practically pure *Trifolium* plus *Phleum* stands. On the other hand, grass leys that have open ditches and are rich in weeds such as *Achillea*, *Alchemilla*, *Hieracium*, *Hypericum*, *Knautia*, *Mentha*, *Prunella*, *Ranunculus*, *Solidago*, *Tussilago* and numerous others, are often very densely populated by the meadow spittlebug. Among the 20 sites of collection there are fields of both types and the floral composition of the leys rich in weeds is very variable, but no correlation between composition of plant communities and composition of polymorphic *Philænus* populations has been observed. Such a correlation, if any, could be established only after extensive quantitative studies.

In the maintenance of polymorphism in *Philænus*, predators probably play a secondary role during larval life. The larvæ of this

insect are all green or yellowish and for the greater part of their lives are protected from sight by the frothy masses of spittle in which they live. Unless different colour forms produce different amounts of spittle, enemies such as prairie warblers (Nolan, 1956), which are guided to the larvæ by the spittle, probably pick up specimens without any discrimination connected with colour patterns.

Without doubt, in many habitats man is the most serious enemy of *Philenus*. Thus, King and Weaver (1953) have noted that the numbers of this insect are affected by meadow management. In Finland, farmers often cultivate hay for 3 or 4 years successively on the same plot. During this period the land is not tilled but after the hay phase it is ploughed and the whole plot used for cultivating cereals. This naturally spells disaster to all the *Philenus* eggs deposited on the fields themselves but not to those laid along ditches or forest fronts. When hay is again cultivated on the plot, the spittlebug population is recruited from the immediate periphery of the field. As stated above, the species has the habit of migrating into open fields after forage crops are cut. This is a habit in all probability favoured by natural selection. Moreover, migrations mean seasonal and relatively abrupt changes of environment. Through disruptive selection, such a change is a potent factor in maintaining genetic diversity, as has been shown experimentally (Thoday, 1959). The dissemination of *Philenus* over open fields during the breeding season is a factor favouring panmixia and also a factor making possible increased biomass production (term by Beardmore *et al.*, 1960) and thus probably promoting fecundity. Perhaps the decrease in relative mean weight observed in the J population after the fields had become inaccessible and the population was confined to the narrow belt of ditch edges is of some value as an argument in this connection.

The present author's own observations show that a considerable proportion of the total copulation occurs soon after the spittlebugs have chosen their sites on the fields from which the hay has been removed. All male forms are able to copulate with any of the female forms, and preliminary observations show no preference trends in choosing a mating partner. In Finland and elsewhere males hatch somewhat earlier than females.

In the beginning of the breeding season, the populations characteristically show a preponderance of male specimens over females, the percentage of males reaching values of over 60 per cent. At around the middle of the adult season, the proportions are fifty-fifty, and thereafter females dominate in steadily increasing proportion. The early hatching of the males means that, up to copulation time, they are exposed to selection for a longer period than the females. Theoretically, any difference between males and females in the proportions of the different forms might be indicative of selection.

In my total material, collected for the most part relatively early during the season, there are 53.6 per cent. males and 46.4 per cent.

females. In the males, the percentage of *trilineata* is 3.25 per cent. (870 specimens) and in the females 2.95 per cent. (686 specimens). This difference is insignificant ($\chi^2 = 2.39$), but since *P* is as high as about 0.10, it is tempting to assume that in general there is selection in favour of *trilineata* during the adult period (and selection against it in winter or during the larval period). To a human eye, *tri* appears to have better protective colouration than many of the other forms.

The N_A samples taken to study seasonal variability in colour form frequencies, although they consistently show an increase in *tri* frequency, are too few to allow any conclusion. The same is true of the data, from Michigan, of Owen and Wiegert (1962). Both the results of Owen and Wiegert and those of the present author rather show that during the adult season selection is very slight, measured with changes in colour form frequencies. Particularly, *typica* does not become rarer during the season, indicating that apostatic selection in the sense defined by Clarke (1962) and others, if operative, is present in the form of a balance between visual selection and a counter-selection which is effective during the adult season.

For the present, it is difficult to estimate the true significance of apostatic selection in the maintenance of polymorphism in *Philænus*. Explaining spittlebug polymorphism, Owen and Wiegert (1962) and Owen (1963) favour this mode of selection. This explanation, although in itself plausible, does not take into account the fact that the seasonally migrating spittlebugs do have two environments and two sets of enemies, including predators. It is quite possible that in the maintenance of colour polymorphism, these abrupt changes of environment are of prime importance. This would imply that a system involving disruptive selection is operative (*cf.* Mather, 1955). In this connection it may be noted that the necessity to change environment, now caused by man's ploughing and sowing, may, in the distant past, have been prompted by grazing herds of big animals.

A study of colour form frequencies during the period of emergence might perhaps reveal changes undetected in samples taken from the populations later during the season (see Creed *et al.*, 1962). Although every one of the colour forms of *Philænus* may correspond to a specific physiological reaction towards a change of environment, the colour patterns themselves are certainly something more than mere markers (Ford, 1961) of genes with invisible effects. Perhaps a combination of Owen and Wiegert's "predator hypothesis" and the present author's "change of environment hypothesis" might constitute a not too bad approximation of the truth.

(ii) *The significance of isolation*

The existence in Aland of *Philænus* populations strikingly different from those living on the mainland has probably been made possible by effective isolation. The people of the Aland archipelago are

Swedish-speaking, in contrast to the Finnish-speaking inhabitants of the neighbouring Turku archipelago and adjoining mainland. For this reason, the economic connections of the people in the Åland isles are mainly internal as regards such dealings as milk routes to dairies and purchases of hay from one village to another.

The rareness of *trilineata* in Åland is probably due to some specific local conditions. The same is perhaps true of the high frequency of *populi* in Åland, as compared with the SWF populations. For the present, with no quantitative data on colour form frequencies in Sweden, it is not possible to say how far the peculiar colour form frequencies in Åland are due to local factors and to what extent they are "geographical" (see below).

Where differences exist between the separate populations of the Åland region, the possible effect of isolation must be seriously considered. In fact, only two of the eleven populations, A and U, are separated by effective barriers from the rest. These populations also differ considerably from the others, being characterised by the lack of some of the forms present in the main island of Åland. Here isolation most probably is an effective factor in the maintenance of the polymorphic balance in the same way as it operates in the Scillies, in their *Maniola jurtina* populations (Dowdeswell and Ford, 1953; Ford, 1955). The effective sizes of the A and U populations are probably too large for genetic drift to gain greater importance than selection.

(iii) *Geographical: the existence of a cline*

Interacting with more local factors affecting *Philenus* polymorphism, there are no doubt geographical factors. The existence of such factors leads to similarities between populations living under corresponding climatic conditions and to dissimilarities along, and especially at the extreme ends of, gradients of change in these conditions. Climatically, Åland and SWF differ greatly from NEF and also from each other. The mean annual temperature is over 5° C. in Åland, 3-4° C. in SWF, but only 1° C. in NEF (Kuusamo). Åland has a lasting snow cover from early January to early or mid-April, but in Kuusamo the fields are snow-clad from early November to mid-May, i.e. twice as long as in Åland. Åland has an almost maritime climate with mild winters and cool summers, the months of May and June being in many years rather dry. The climate of Kuusamo is continental, and the midsummer (July-August) in Kuusamo does not differ much from Åland in total insolation, the more intense radiation in Åland being partly compensated by the longer length of the day (18 hours in Åland in early July, 23 hours in Kuusamo).

In Åland, the habitual early summer droughts often render vast areas of fields yellowish brown over most of July. Against this background, *populi* is probably the most effectively protected form, and therefore it is quite possible that the high frequency of *pop* can be

explained by a high selective value under visual selection. This hypothesis is parallel to that offered by Cain, King and Sheppard (1960) to account for the distribution of colour forms of *Cepæa nemoralis* in Europe.

Although Määttä and Kuusamo are not the northernmost populations of *Philænus*, they can safely be called peripheral isolates (Mayr, 1954) since habitats available to this species in Lapland are isolated and scattered in the wide expanse of forest. It is not surprising that the cline in climatic conditions described above is reflected in *Philænus* colour form frequencies. Levins (1963) has tabulated factors affecting polymorphism and has found that a pattern along geographic gradient in niche frequency, together with heterogeneity of the environment in time, is able to lead to a cline in the proportions of some polymorphic types. This is exactly what has been observed with the dark forms of the spittlebug.

A general increase in the frequencies of the heavily pigmented forms leads to a decrease in the frequency of *typica*: in males from 95.2 per cent. in SWF to 81.7 per cent. in NEF, and in females from 77.5 to 63.4 per cent., respectively.

(iv) Possibilities of genic determination

The difficulty of breeding *Philænus* in captivity has thus far prevented a solution of the problem of genic determination by direct crossing experiment. According to Owen and Wiegert (1962), C. R. Weaver has succeeded in obtaining offspring from known females with mating partners unknown. The general result was that the forms tend to reproduce themselves, a result useless as a basis of any hypotheses but important in proving that genic determination does exist.

With due caution, hypotheses based on indirect evidence may be framed. The fact that, on the wings of the insect, unpigmented fields belonging to the *v* series and those belonging to the *f* series seldom occur together (among the 13,400 females collected in 1963 there were 3 specimens combining the *qua* and *lat* markings) has two possible explanations. First, the *v* and *f* factors may belong to a multiple allelic system, and second, that epistasis exists. An attempt to explain all features on the multiple allelic basis was made by Halkka (1962b).

The rareness of certain forms in Åland cannot be explained on the assumption that the *populi* factors prevent other patterns from appearing. In the U.S.A. high frequencies of *trilineata* are found together with high *populi* in Wisconsin (Fisher and Allen, 1946), and in England along a ridge on the Pennines the highest percentage of *tri* ever observed has been found in a population which had a high proportion of *pop*, too (Whittaker, unpublished).

5. SUMMARY

Seasonal, annual, spatial and geographical variability in the balanced polymorphism of *Philænus spumarius* has been studied in

Finland. The slightness of seasonal variability shows that during the adult life there is probably no strong selection by predators involving different selective values of the phenotypes. Annual changes do occur and show that polymorphism is of the oscillating type, but the amplitude of this oscillation is confined within limits such that a difference between the extremes seldom reaches formal statistical significance.

The limits mentioned are set by geographical factors. The presence of a cline in the frequencies of the colour forms has been shown, heavily pigmented forms increasing northeastwards.

The effect of isolation is evident on the populations of the outlying islands of the Åland archipelago. Here a system parallel with that found in the *Maniola* studies is operating.

As a key hypothesis of the present work, the idea is presented that seasonal migrations of the meadow spittlebug, including a change of environment, are largely responsible for the maintenance of polymorphism in this insect.

Possible genetic systems operative in *Philæus* polymorphism are briefly discussed.

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