THE POLYMORPHISM IN *PHILAENUS SPUMARIUS* (L.) (HEMIPTERA: CERCOPIDAE) IN BRITISH COLUMBIA

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ABSTRACT

This paper analyses the distribution and relative frequency of the morphs of **Philaenus spumarius** in British Columbia, the populations being drawn from different biotic areas. It is shown that nine morphs occur in the province and of these, **marginellus** occurs only in the south-west corner; **marginellus** and **lateralis** occur only as females. The frequency of the morphs in the biotic areas of the province is not uniform; populations in dry areas differ significantly from those in wet areas. Populations taken from the various forest areas are not identical, nor are those from coastal **areas**.

Within a single biotic area, the frequency of morphs appears to be stable. No significant difference was determined between two samples taken sixteen years apart. Further, there appears to be no significant seasonal, daily or hourly change in the morph frequency in an area.

An experiment carried out on mating individuals failed to demonstrate a tendency for non-random mating and there was no evidence for the preferential mating of the rarer types.

INTRODUCTION

The Meadow Spittlebug, Philaenus spumarius (L.) is a common Holarctic insect which in the adult instar, exists in a number of distinct colour forms. The insect is able to utilize almost any succulent foliage, and has been recorded from over 400 species of plants (Doering, 1930a, 1930b). It is injurious to many crops and commercially may reduce hay yields by 20 to 50 per cent (Gyrisco, 1958; Anon, 1962), and stunt or kill individual legume plants (Weaver & Whitney, 1958). The biology has been studied by Weaver & King (1954) and Levigne (1959), while Wiegert (1964) has studied the population energetics and Halkka (1962a, 1962b), Owen & Wiegert (1962) and Hutchinson (1964) the morph frequency.

The polymorphism exhibited by this species seems to be stable, although it is little understood at present. Boring (1913) studied the various forms and could find no corresponding variation in the karyotype. Halkka (1962b) suggested that two or three colour inhibitor genes may be involved, some connected wth "sex determiners", and Owen & Wiegert

(1962) suggest that some are sex linked. Hutchinson (1964) says that it seems not unlikely that a multiple allelomorphism is involved. Halkka et al. (1966) have recently carried out some crossing experiments and conclude that six major genes are involved and that "The six major genes may be allelomorphic with each other". There is a "possibility that the six major genes constitute a dominance hierarchy", and five of the genes "always manifest their effects in the female but never in the males" while the seventh "has a dominant mode of inheritance in both sexes". Halkka et al. (1966) further state that "The expressivity of the six major genes is remarkably independent of external factors, including food plants of the P and F_1 generations".

Hutchinson (1964) has stated that "While no clear understanding of the whole situation, which may prove to be one of the most dramatic examples of polymorphism, will be possible without g e n e t i c knowledge, more geographical and ecological information is sorely needed". This paper describes some observations on P. spumarius in British Columbia.

MATERIAL AND METHODS

Material in the Spencer Entomo-

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logical Museum at the University of British Columbia was studied to determine the distribution and frequency of morphs throughout the Province and to determine variations between different biotic areas. Some large collections made several years apart enabled a comparison of populations over a period of 16 years. Further, field collecting was done to study possible variation in morph frequency with season and over short periods of time.

An experiment to test the randomness of mating was performed on adult insects collected in August 1966, from a 15 yard by 60 yard area of vegetation at the University of British Columbia: the main plants on the area were *Plantago*, *Dactylis* and *Trifolium*. Field collected insects were placed in a cage containing cardboard strips for a resting surface. Mated pairs were removed in the first 30 minutes of the experiment and were kept is ol a ted in individual 3" x 1" shell vials stoppered with cotton. All mated pairs were formed in the first 30 minutes of the experiment, and such pairs were found to remain *in copula* from 30 minutes to two hours. A number of mating pairs were also obtained in the field, but there were too few for analysis.

The morphs were determined according to the patterns given in Halkka (1962a) and specimens compared with material taken in Finland and England. We have called the morph which is brownish with two pale costal spots on the corium, *spumarius*: this follows Edwards (1896) and the practice of most North American authors (Weaver & King, 1954; Owen & Wiegert (1962).

The biotic zones recognized in the paper follow the scheme of Munro & Cowan (1947). The main climatic features of these various zones are given in Table 1.

The method of Skory (Steel & Torrie, 1960, p. 368) was used in most calculations. Because of the scarcity of some morphs, lumping, as recommended by Siegel (1956), was necessary to operate the Chi-square test.

BIOTIC ZONES	ANNUAL PRECIPITATION (inches)	TEMPERA Mean Minimum	ATURE (°F) Mean Maximum	FROST FREE DAYS
Dry Forest	10-20	10-20	80-90	150 - 175
Cariboo Parklands	15-20	5-10	70-75	50.100
Columbia Forest	35-50	15 - 25	80-85	100-150
Subalpine Forest	40-50	—10 to 5	68-70	50-100
Coast Forest		30-35	60-70	200 - 250
Gulf Island	25-35	30-35	70-75	230 - 275
Puget Sound Lowlands	35-60	20 - 30	70-75	200-250
Queen Charlotte Is. (Ma	assett) 71.11	20.5	65.0	168

TABLE 1-Climatic data for various biotic zones in British Columbia.

RESULTS

a. Distribution and frequency of morphs

Nine different morphs were recognised in the material from British Columbia (Table 2). Of these, *marginellus* has been taken only in the Gulf Islands area (Victoria) and the Puget Sound Lowlands (Vancouver). The other morphs are fairly widely distributed. While the total number of males and females studied was about equal, both *lateralis* and *mar*- ginellus were recorded only as females.

Table 3 gives the number of the various morphs from each biotic area studied; the Gulf Islands data are omitted since the sampling was known to be non-random. Analysis of the data in Table 3 show that the samples cannot be considered to have come from a single population (χ^2_{+15} = 70.026; p \ll 0.001).

While statistically it is not acceptable to reanalyse these data in vari-

				MORP.	H TYI	PES			
BIOTIC ZONE	leucophthalmus	leucocephalus	lateralis	marginellus	fasciatus	spumarius	typicus	trilineatus	populi
Dry Forest	х	x	х		х	x	х	х	х
Cariboo Parklands		x			х	х	X	х	x
Subalpine Forest		х			х	X	х	х	х
Coast Forest		x	Х		X	х	х	х	X
Gulf Islands	х	X	Х	х	х	х	х	х	х
Puget Sound Lowlands	X	х	Х	х	X	х	Х	х	х
Queen Charlotte Islands						х	х	х	х

TABLE 2-Distribution of morphs of Philaenus spumarius in British Columbia.

ous groupings, a case can be made from the biological point of view for doing so. We know that the various biotic zones in the province are climatically quite different and it is reasonable to ask if the polymorphism is different in these areas. Table 4 presents some comparisons which have been made. There would appear to be no difference between samples taken from populations within the wet areas (Queen Charlotte Is. + Coast Forest) and those from populations in dry areas (Cariboo Parklands + Dry Forest). However, populations in coastal areas appear to be dissimilar as do those in forest areas: the Dry Forest area is largely grassland and so was not included in the 'All Forest' analysis. b. Stability of morph frequency.

The stability of the morph frequency with time was studied by comparing two collections taken at Merritt in the Dry Forest area 16 years apart. Table 5 indicates that the two samples were not significantly different. This probably indicates a marked stability in the polymorphism, at least in this area.

Two samples taken at Burnaby in the Puget Sound Lowlands were compared to see if there was a seasonal change in the morph frequency in this area. The sample taken on 14 November 1962 was not significantly different from that taken on 29 July 1962 (Table 5). A similar comparison of catches taken on two consecutive days in September 1962 showed no significant difference.

Finally, to see if there was a change in morph frequency with temperature, photoperiod or other similar daily change, two samples were compared. The sample taken

TABLE 3—Number of various morphs of Philaenus spumarius in different populations in British Columbia.

BIOTIC ZONE	leucophthalmus	leucocephal	lateralis	margi ne llus	MORP fasciatus	H TYP spumarius	typicus ES	trilineatus	populi	
	mus	lus								Total
Dry Forest	3	9	2	0	7	129	175	47	20	392
Cariboo Parklands	0	3	0	0	1	20	35	6	4	69
Subalpine Forest	0	4	0	0	9	110	127	9	12	271
Coast Forest	0	2	7	0	9	95	93	68	1	275
Puget Sound Lowlands	3	22	3	1	31	239	195	70	6	570
Queen Charlotte Islands	0	0	0	0	0	11	2	8	3	24

1601

GROUP All of B.C.	D BIOTIC ZONES All zones	EGREES OF FREEDOM 15	CHI-SQUARE 70.026	<< 0.001
Low Coastal Area	Queen Charlotte Is. Coast Forest Puget Sound Lowland	6 Is	56.485	<< 0.001
Wet Coast	Queen Charlotte Is. Coast Forest	3	1.196	0.7-0.5
Dry Interior	Cariboo Parklands Dry Forest	3	0.461	0.95-0.90
Dry Interior + Dry Coast	Cariboo Parklands Dry Forest Puget Sound Lowland	6 Is	17.527	0.01-0.001
All forest	Subalpine Forest Coast Forest Queen Charlotte Is.	6	75.240	<< 0.001

 TABLE 4—Difference between populations of Philaenus spumarius from various areas in British Columbia.

around 14:00 hours did not differ significantly from that taken around 18:00 hours (Table 5).

c. Randomness of mating

Table 6 presents the data obtained from 24 mated pairs in the laboratory mating experiment. An analysis of these data suggest that the mating is random (χ^2 (4) =4.944; 0.30 p 0.20). Further, a comparison of these data with the expected pairing based on the frequency of morphs in the original population, indicates that the pairs obtained were randomly drawn from the population ($\chi^2_{(4)} = 7.43$; 0.20 > p > 0.10).

DISCUSSION

Hutchinson (1964) says that P. spumarius may constitute one of the most dramatic examples of polymorphism in animals, but a survey of the literature shows that it has not so

	TABLE 5C	Comparison o	f sam	ples	of P	hilae	nus spum	narius.		
					OUF		TOTAL		CHI2	р
(1)	Samples taken 16 year Merritt 2	s apart 0.viii.32	3	12	29	4	48	3	4.1	0.3-0.2
	Merritt 1	5.viii.48	11	19	34	11	75	ъ	4.1	0.3-0.2
			14	31	63	15	123			
(2)	Samples taken 3 mont Burnaby	hs apart 29.vii.62	8	8	6		22	2	0.98	0.7-0.5
	Burnaby	14. x. 62	3	6	5	100000000000000000000000000000000000000	14	2	0.90	0.7-0.0
			11	14	11		36			
(3)	Samples taken 1 day a Burnaby	apart 7. ix. 62	7	29	15	3	54	3	4.5	0.3-0.2
	Burnaby	8. ix. 62	4	16	18	6	4 4	U	1.0	0.0 0.2
			11	45	33	9	98			
(4)	Samples taken 4 hours Burnaby 7.ix	s apart .62 (14:40 pm	1) 7	29	15	3	54	3	5.3	0.2-0.1
	Burnaby 7.ix	.62 (18:40 pm	n) 6	15	19	6	46	3	0.0	0.4.0.1
			13	44	334	9	100			

48

TABLE 6 — Mating pairs of Philaenus spumarius obtained in Laboratory experiment. Original population: 39 & 51 \heartsuit spumarius, 11 & 12 \heartsuit trilineatus, 8 & 15 \heartsuit populi.

			Males	
		spumarius	trilineatus	populi
	spumarius	11	3	1
Females	trilineatus	3	3	0
	populi	1	1	1

far been recognised as such, being absent from the reviews of Ford (1965a, 1965b). Halkka *et al.* (1966) have shown that the polymorphism has a genetic basis, but it is clear that much remains to be learned about the situation. The present information suggests that the genetic control is not a very simple one.

A study of the various morphs in British Columbia and the comparison of these with specimens from eastern North America and western Europe, shows that there is considerable variation in the colour pattern of the types. The same morphs from different parts of the range of this insect, appear slightly different and it is not always easy to separate them.

The present study shows that the morph frequency is not the same throughout British Columbia, and suggests that there is a difference between populations in dry and in wet areas. While climate would appear to have some effect on the polymorphism, it is not possible to define the environmental factors more precisely at the present time. Since no change was detected between samples taken at different times of day, the situation in P. spumarius would seem not to be so simple as that in Colias (Lepidoptera), where Hovanitz (1953) has shown a correlation with temperature.

We were unable to detect a seasonal change in the morph frequency in an area. Owen & Wiegert (1962) working in Minnesota likewise found no seasonal variation in the frequency of *populi* (= *pallidus*) and *spumarius*. On the other hand, Dobzhansky (1943, 1948) working on *Drosophila* and Timofeef-Ressovsky (1940) working on *Adalia* have shown marked seasonal variation in the polymorphism in these insects.

The fact that two samples taken in the same area over a 16 year period showed no significant difference, can be taken to indicate that the polymorphism is probably stable, at least in that area. Owen & Wiegert (1962) showed a similar stability over a four year period in an abandoned field in southeastern Michigan. However, studies on the frequency of morphs over long periods in other animals have usually demonstrated marked changes (see Dobzhansky, 1958; Komai, 1956; Clark & Murray, 1962a, 1962b).

There seems to be little predation on *spumarius* populations (Weaver & King, 1954) and thus the selection would appear to be rather different from that described in *Biston betularia* (Lepidoptera) (Kettlewell, 1961) and *Cepaea* (Mollusca) (Cain & Sheppard, 1954). Nevertheless, Owen & Wiegert (1962) state that the relative frequency of the forms may be determined through selection by predators.

In the experiment on randomness of mating, the results seem to indicate that mating is indeed random. Thus preferential mating, which is reported to occur in *Panaxia dominula* (Lepidoptera) (Sheppard, 1952) seems not to be present in *P. spumarius*. Further, there is no evidence that there is any preferential mating of the rarer types, as recently suggested in *Drosophila* by Ehrman *et al.* (1965).

Thus our study indicates that factors cited as the main selection forces in other examples of polymorphism, seem not to apply in *P. spumarius*. At the present time, one can only state that the selective advantage of the polymorphism in this insect is unknown. The results obtained so far on populations in British Columbia suggest that further studies on the temperature and humidity preferences and tolerances of the various morphs may be worthwhile.

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MOISTURE AND FAT CONTENT DURING THE ADULT LIFE OF THE AMBROSIA BEETLE, TRYPODENDRON LINEATUM (OLIV.)

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ABSTRACT

Depletion of fat deposits during the long hibernation period of the adult ambrosia beetle, **Trypodendron lineatum** (Oliv.), amounts to about one quarter of the original fat content. The fat loss during flight activity appears to be also about one quarter of the amount present at the start of hibernation.

Experiments with beetles stored at different temperatures indicate that during a long cool spring the rate of fat loss increases, probably affecting the vigor of the population during subsequent flight and brood establishment.

INTRODUCTION

Many insects derive energy for metabolic activity from stored lipids (Fast, 1964), supplies of which are likely to vary during adult life. To understand individual behaviour patterns, a knowledge is required of the relationship between the fat content of the insect and its behaviour. Atkins (1966) demonstrated such a relationship in a scolytid, and stressed the need for studies that penetrate to the physiological basis of behavioural variation.

The ambrosia beetle, *Trypondendron lineatum* (Oliv.), spends a major part of its adult life in hibernation. Climatic conditions in fluence the length of the hibernation period and thus affect the utilization of stored lipids which in turn affects the subsequent flight and attack activities. This investigation was undertaken to learn more about the depletion of fat during hibernation and the flight period that follows.

METHODS AND MATERIALS

The data were obtained from beetles collected from duff or bark in standing timber around logging areas near Lake Cowichan, B.C., between August 1965 and July 1966 (Dyer and Kinghorn, 1961). The heated pan method described by Hadorn (1933) and Kinghorn and Chapman (1959) was used for recovering the beetles. Moisture and fat were determined by drying in an oven and extracting with petroleum ether in a Soxhlet unit (Nijholt, 1965). In this presentation, values for fat, or lipids, represent substances extractable in petroleum ether.

To check the speed and efficiency of the extraction, groups of 25 beetles were dried, weighed, and extracted for various lengths of time up to six hours. The amount of fat loss

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