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Genetic drift and patterns of diversity among colour-polymorphic populations of the homopteran *Philaenus spumarius* in an island archipelago

PAUL M. BRAKEFIELD

Section of Evolutionary Biology, Department of Population Biology, University of Leiden, Schelpenkade 14a, 2313 ZT Leiden, The Netherlands

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Populations of the sedentary spittlebug *Philaenus spumarius* were sampled on 26 islands in the Isles of Scilly archipelago. The islands vary in size from 0.2 to 662 ha. Patterns of phenotypic and genic diversity at a melanic colour-polymorphic locus are examined. The indices of diversity were characterized by a comet-shaped distribution when plotted against island area with increasing uniformity among larger islands. A similar pattern occurred in a plot against the first principal component from analysis of nine independent island variables, including area. The greater diversity among smaller islands was associated with the absence of melanics (and thus of rare alleles) on some of them and a generally higher variance in allele and phenotype frequencies. There was no overall loss of heterozygosity. One melanic allele (l) occurred at a *substantial* frequency on one of the smallest islands even though it was not detected anywhere else. Patterns of population density, island vegetation and height suggest that small-island populations are likely to experience bottlenecks or extinction-recolonization cycles. The observations are consistent with a major role of intermittent drift and founder effects among the smaller islands. The results are compared with those of Halkka and his co-workers for islands in the Gulf of Finland.

KEY WORDS:—Genetic drift – founder effects – diversity indices – island differentiation – Isles of Scilly – polymorphism – melanism – *Philaenus spumarius*.

CONTENTS

INTRODUCTION

Natural selection, random genetic drift, gene flow and mutation are the four major processes used by population geneticists to model changes in allele

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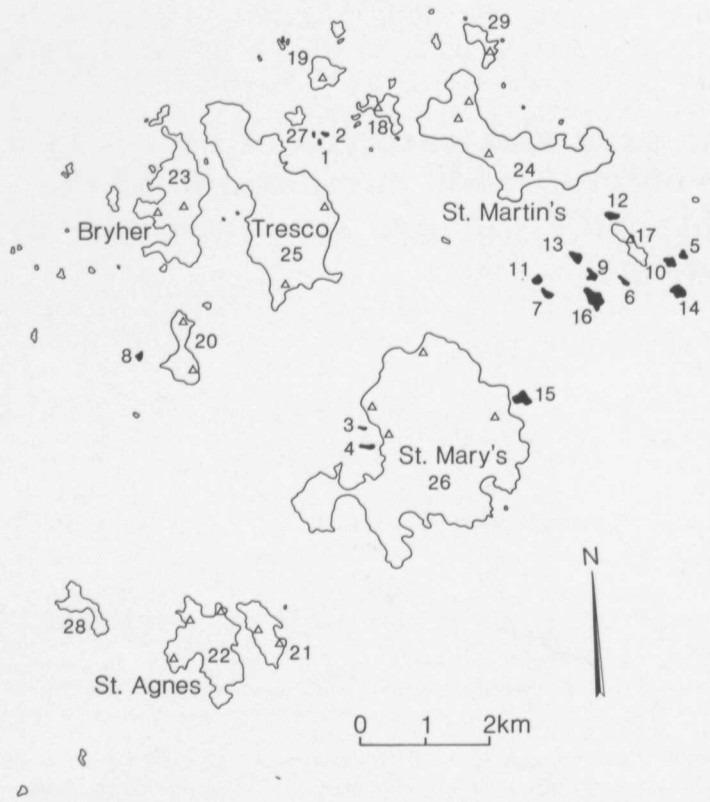

Figure 1. Map of the Isles of Scilly. All islands which were visited are numbered with those of less than 5 ha in black. Triangles show sites from which samples were obtained on islands larger than 10 ha. For names of all islands see Appendix.

frequencies in evolution. Many studies have examined natural selection or quantified migration rates in the wild (Endler, 1977, 1986) and mutation rates are known for some gene loci. Although the dynamics of genetic drift are well understood from theoretical work (see Nei, 1987) and have been examined in laboratory populations (e.g. Buri, 1956; Dobzhansky & Pavlovsky, 1957; Rich, Bell & Wilson, 1979; Wool, 1987), information from natural populations is comparatively sparse and has often involved allozyme variation in island populations (Janson, 1987 and work cited in Wool, 1987). Recent interest in islands has concentrated on the factors determining species diversity although they also provide excellent opportunities for investigating effects on diversity within species (Berry, 1983).

This study is of colour polymorphism in populations of a sedentary insect, the meadow spittlebug *Philaenus spumarius*, on islands varying in area from 0.2 to 662 ha in the Isles of Scilly about 40 km off the south-west coast of England. This homopteran exhibits eleven widely-distributed non-melanic and melanic phenotypes controlled principally by seven alleles at a single locus (Halkka *et al.*, 1973). Such polymorphisms are usually considered to be influenced primarily by selection and gene flow (e.g. Brakefield, 1987) but field studies have seldom involved circumstances likely to be associated with strong effects of stochastic

processes (but see Halkka *et al.*, 1970; Goodhart, 1973; Cameron & Dillon, 1984; Johnson, 1984; Oxford & Shaw, 1986; Oxford, 1989). The following more specific questions are addressed in the present study. First, what relationships exist between the phenotypic and genetic variation and the variables describing island size, isolation and habitat? Second, is there any change in diversity among populations with island (population) size? Third, do the observed patterns reflect real biological effects or are they the result of an artifact introduced by variation in sample size? Laboratory experiments with insects polymorphic for colour markers illustrate the dispersion of allele frequencies expected in small populations due to increased sampling error (Buri, 1956; Rich *et al.*, 1979; Wool, 1987). The results of the present study are compared with the data of Halkka *et al.* (1970) for *P. spumarius* on islands in the Gulf of Finland.

Evolutionary studies of wing spotting in the butterfly *Maniola jurtina* on the Isles of Scilly (reviewed in Ford, 1975) rose to prominence with the selection-drift controversy. Ford and his co-workers argued that their data demonstrated selection of a gene complex adapted to a variety of habitats on each of the three largest islands. Their finding that populations on smaller islands tended to differ from one another and from those on the three large islands was accounted for by selection in these populations in response to particular and specialized environments. Dobzhansky & Pavlovsky (1957) and Waddington (1957) argued that the results could also be explained by founder effects or intermittent bottlenecks and drift. Murray (1966) found some differences between islands in patterns of linkage disequilibria for shell colour and banding polymorphism in populations of the snail *Cepaea nemoralis*. Both the butterfly and the snail are more or less restricted to larger islands in the archipelago while populations of the spittlebug can occur even on islets with less than 50 m^2 of vegetation.

MATERIALS AND METHODS

The Isles of Scilly and collection of samples

Most of the islands in the Isles of Scilly (Fig. 1) were probably formed some 1500 years ago from a single granitic land mass by a continuing increase in sea level, possibly combined with breaches of an outer ring-shaped area of higher ground by a great storm (Thomas, 1985). Since *P. spumarius* is univoltine any genetic differences between islands are thus likely to have arisen in less than about 1500 generations. Isolation by long distance is not a feature of the islands. Thus the mean distance to the nearest island for the twenty-one islands of less than 40 ha and from which large samples were obtained is 160 m (range: 40–400 m).

In July 1986 vegetation was swept with a stout net on twenty-nine islands (Fig. 1) to collect samples of adult *P. spumarius*. Collecting covered different areas of the vegetation at each site. Most samples were large (mean = 492). The insects were sexed and scored using a binocular microscope (data in Appendix). Two to four samples were collected at different sites on each of the seven largest islands to examine heterogeneity within islands. Single samples were obtained from nineteen smaller islands. A sample which was too small for analysis was obtained on a short visit to White Island (number 29) off St. Martin's. Two other islands yielded no *P. spumarius* during long searches. The small Crow's Island (27) was

very thoroughly searched while only part of the vegetation on the larger island of Annet (28) was covered.

The polymorphism, measures of diversity and data analysis

The most abundant phenotypes were the three non-melanics: mottled brown *typicus* (TYP), pale *populi* (POP) and striped *trilineatus* (TRI) (full list of names and abbreviations in Appendix). Melanics (MEL) accounted for about 4% of all females (209 of 5289) and 0.1% of all males (seven of 7492). Scoring of the phenotypes was standardized on the system used by D. R. Lees' group at Cardiff. Several male melanics were difficult to score. The distinction between the TYP and POP phenotypes was also sometimes unclear, as was that between very dark TYP and poorly marked melanics, especially of the *flavicollis* (FLA) form, in a few insects. The phenotypes were grouped into three classes (TYP+POP; TRI; MEL) in tests of heterogeneity.

In order to examine genic diversity (or strictly speaking allelic diversity) the following assumptions, based on the breeding work of Halkka *et al.* (1973) and Stewart & Lees (1987, 1988), are used: (1) the top dominant *T* allele in each sex controls the TRI phenotype, (2) melanic phenotypes are controlled by a single Me allele of intermediate dominance in females and recessive in males and (3) the TYP and POP phenotypes are controlled (principally) by the *t* allele which is recessive in females and of intermediate dominance in males. Estimation of allele frequencies (see Crow, 1986: 13) then assumes that populations are in Hardy-Weinberg equilibrium. Although several melanic alleles occur in the Isles of Scilly (see the Discussion) the second assumption involving a single melanic allele is unlikely to significantly bias estimates of heterozygosity because of the rarity of melanics and the predominance of the *marginellus* (MAR) form controlled by the *M* allele. The nearly complete limitation of melanics to females in the Isles of Scilly is characteristic of the polymorphism throughout much of the species' range including Finland (see Stewart & Lees, 1988). It suggests that the genetics of the polymorphism is also similar to that in Finland (Halkka *et al.*, 1973). Estimation of allele frequencies from the total samples for the Isles of Scilly yields $T=0.1016$, $\mathrm{Me}=0.0223$ and $t=0.8761$ in females and $T=0.0883$, $\mathrm{Me}=0.0306$ and $t=0.8812$ in males. The reasonable correspondence between the sexes in the estimated frequencies of the 'melanic allele' is consistent with a reversal of dominance. However, when the occurrence of the individual melanic phenotypes, both in the Isles of Scilly (Appendix) and elsewhere, and their patterns of inheritance are considered, it appears that some other mechanism involving variable penetrance and/or expression of the melanic alleles plays at least some part (see discussion in Stewart & Lees, 1988). Moreover, in some British populations, especially in certain industrial regions of South Wales, the pattern of inheritance across the sexes is different and melanic phenotypes are much more frequently expressed in males (Stewart & Lees, 1987, 1988).

The following three diversity indices were calculated for each sex in individual populations (minimum sample size=25): phenotypic diversity based on a Shannon index where $H_p=-\Sigma p_i.\log_2 p_i$ and p_i is the frequency of the ith individual phenotype; equitability $=H_p/H_{\mathrm{maximum}}$; genic diversity using a measure of heterozygosity, $H_g=1-\Sigma a_i^2$ where a_i is the frequency of the ith allele as

described above. The variance of each value of H_p was estimated directly from the data by application of the formula given by Hutcheson (1970).

Initially the frequency data were analysed against island area. Other independent variables were then examined in multivariate analyses for additional powers of explanation. The island variables of area (see Appendix), perimeter length, maximum height above mean sea level, shape as measured by the deviation from a perfect circle on a scale from 1 to 0, distance to nearest island larger than about 0.1 ha and distance to nearest island larger than 100 ha were all taken from the Ordnance Survey outdoor leisure map number 25 using an IMAGAN image analysing system. Other variables were: vegetation type as distinguished in the field by recognition of seven categories based on a crude scale of increasing 'complexity of vegetation structure' from very simple plant communities (see below) to mixed meadow grassland and low bramble-gorse scrub; density of *P. spumarius* as estimated on a five-point scale from records of captures per sweep of standard length; relative frequency of the related grassland spittlebug *Neophilaenus lineatus* which was collected in low (1–46) or high (121–327) numbers on 16 islands.

RESULTS

The analysis concentrates on data for females because of the greater diversity within populations of this sex (see Appendix). Results were similar for males as is indicated by selective citing of analyses in this sex.

Distribution of the phenotypes

The results of heterogeneity tests on the separate samples from each of the seven largest islands show that phenotype frequencies were homogeneous in each sex within six of the islands (Table 1). As in other heterogeneity tests for females the interpretations are not influenced by excluding the melanic class from analysis. There is, therefore, little indication of any substantial differentiation within larger islands.

Figure 2 shows the frequency of the phenotype classes on individual islands. There is a consistent trend in each sex towards comet-shaped distributions with

TABLE 1. Heterogeneity chi-square analysis of multiple samples of *Philaenus spumarius* from larger islands in the Isles of Scilly

Island	Area (ha)	No. of samples	Females			Males		
			χ^2	d.f.	P	χ^2	d.f.	P
Sampson	35	2	3.13	2	NS	1.20	1	NS
Gugh	36	2	0.18	2	NS	7.32	1	**
St Agnes	109	3	12.16	4	*	5.68	2	NS
Bryher	130	2	4.69	2	NS	3.74	1	NS
St Martin's	228	3	5.58	4	NS	1.85	2	NS
Tresco	301	2	0.83	2	NS	0.14	1	NS
St Mary's	662	4	3.37	6	NS	7.21	3	NS

Females grouped by TYP + POP : TRI : MEL phenotype classes and males by TYP + POP : TRI (see text).
*$P<0.05$; ** $P<0.01$.

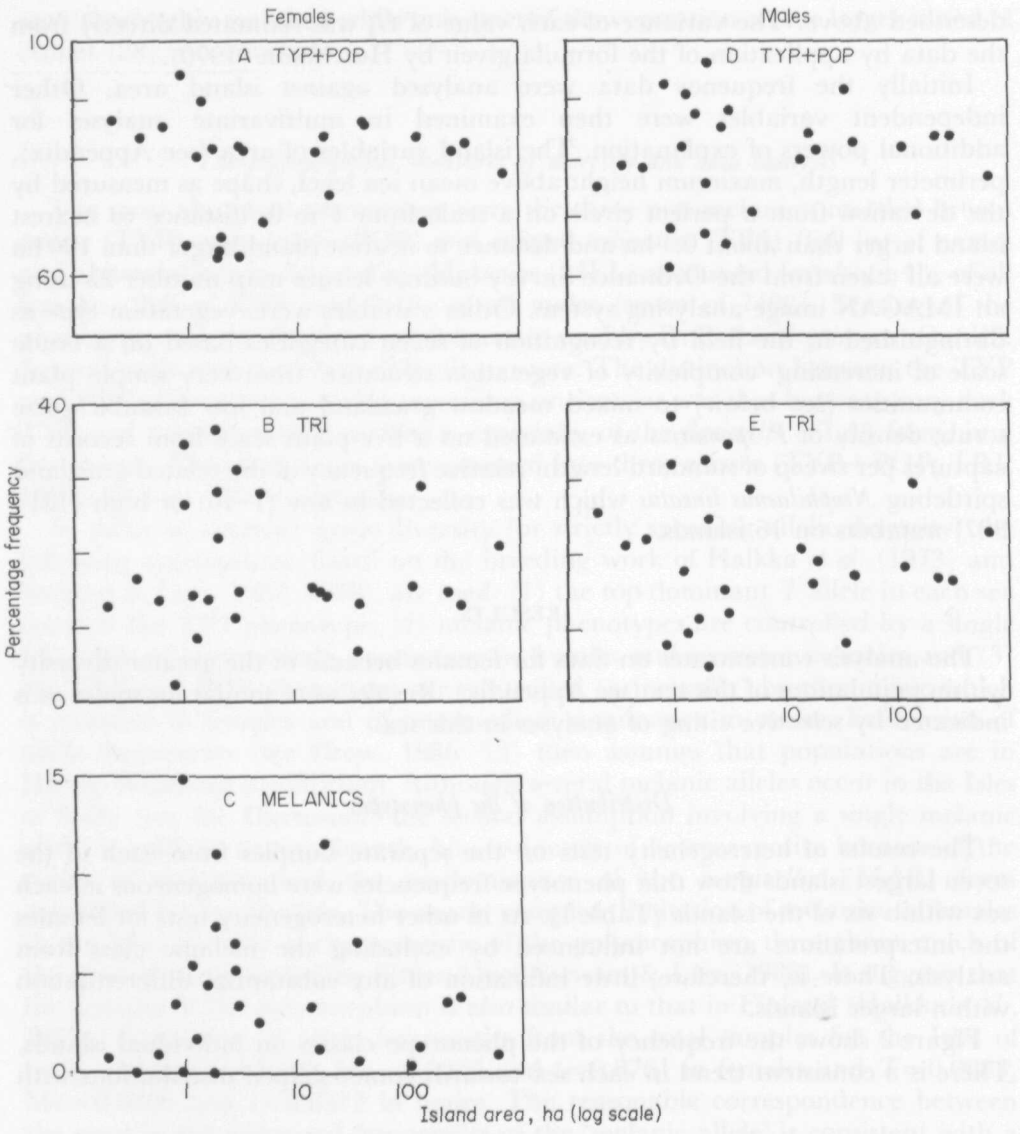

Figure 2. Frequency of the three major groupings of phenotypes (see text) in samples of female and male *Philaenus spumarius* from the Isles of Scilly.

greater dispersion of values for the smaller islands. Table 2 shows that this is reflected in substantially greater heterogeneity between populations of the smaller islands in each sex, although there are significant differences even among the largest islands. A corresponding analysis of genic diversity (Nei, 1987) shows that differentiation between islands accounts for about three to four times more of total diversity for the smaller, than the larger islands (Table 3). However, the coefficient of between-island differentiation is consistently less than 5%.

The frequency distributions for the TRI and MEL phenotype classes in females on the ten islands larger than 10 ha are shown in Fig. 3. Melanics occur on each of these islands but constitute less than 4% of females except on St.

TABLE 2. Heterogeneity chi-square analysis of phenotype frequencies in samples of *Philaenus spumarius* from islands grouped by area

Area (ha)	No. of islands	Females			Males		
		χ^2	d.f.	P	χ^2	d.f.	P
0–1	6	285.44	15	***	74.60	5	***
1–2	6	156.79	15	***	67.68	5	***
2–5	4	23.75	9	**	55.97	3	***
10–40	5	41.84	12	***	20.01	4	***
100–700	5	38.59	12	***	26.72	4	***

Females grouped by TYP+POP : TRI: MEL phenotype classes and males by TYP+POP : TRI (see text).
** $P<0.01$; *** $P<0.001$.

Helen's (19) and Sampson (20). The greater variability among smaller islands (<5 ha) is evident in Fig. 4. In particular, the eleven islands in the compact group of the Eastern Isles are highly heterogeneous (females: $\chi^2=186.0$, d.f.$=20$ and males: $\chi^2=117.2$, d.f.$=10$ with $P\ll0.001$ in each case; this group includes the smallest of the larger islands). Female melanics were at a frequency of higher than 4% on seven of these islands. They were most abundant (14.9%) in a large sample from Ragged Island (6) where an extremely high population density was associated with a very simple plant community dominated by a species of *Atriplex* and *Beta maritima*. However, 72 of the 74 melanics from this island were the distinctive *lateralis* (LAT) phenotype (see Fig. 4) controlled by the *L* allele (Halkka *et al.*, 1973). LAT was not collected on any other island. A further melanic phenotype, *flavicollis* (FLA), is at a low frequency in the Isles of Scilly and seems to show a patchy distribution which includes several of the Eastern Isles (Figs 3 & 4). The *marginellus* form was collected on each of the 23 islands where melanics were found.

No melanics were collected on two closely neighbouring islands, the Innisvouls, in the Eastern Isles or on Foreman's Island (2) close to Tresco. The large samples (230 to 343 females) involved suggest that melanics were probably absent on each island. For example, combining across Little and Great Innisvouls (5 & 10) and applying the binomial distribution, the predicted phenotype frequency at which the probability of collecting at least one melanic female was greater than 95% is 0.55%.

TABLE 3. Analysis of genic diversity in the Isles of Scilly populations of *Philaenus spumarius* grouped by island area

Island area (ha)	Number of islands	Females			Males		
		H_T	H_S	G_{ST}	H_T	H_S	G_{ST}
0.2–1	6	0.2070	0.1972	0.0471	0.2287	0.2226	0.0264
1–2	6	0.2474	0.2405	0.0277	0.1619	0.1562	0.0348
2–5	4	0.2476	0.2431	0.0184	0.2124	0.2067	0.0270
10–40	5	0.1731	0.1717	0.0083	0.1513	0.1501	0.0078
100–700	5	0.2007	0.1987	0.0102	0.1957	0.1938	0.0094

Genic diversity: H_T, total diversity; H_S, between-island diversity; G_{ST}, coefficient of between-island differentiation.

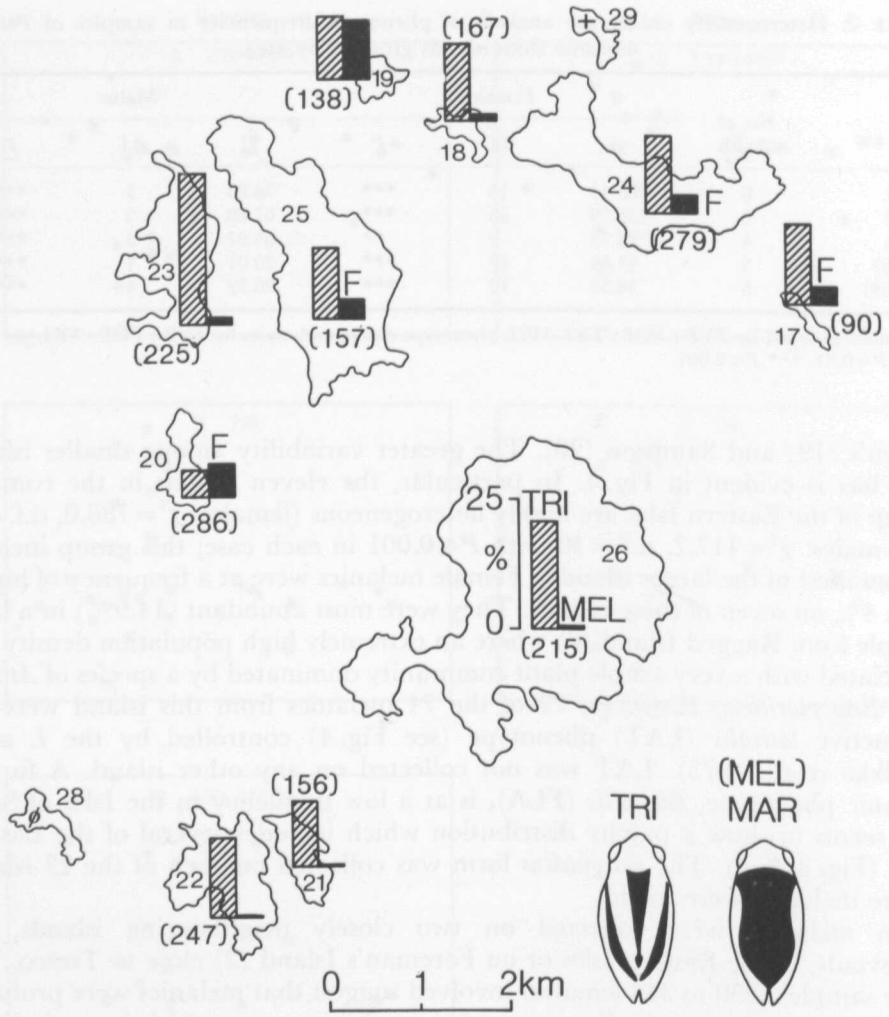

Figure 3. Frequency of *trilineatus* (TRI = hatched bars) and melanics (MEL = solid bars) in samples of female *Philaenus spumarius* from islands larger than 10 ha in the Isles of Scilly. The remainder of the samples are pale non-melanics (TYP + POP). F = presence of *flavicollis* melanics; + = small sample; ϕ = none collected. Map numbers are given (see Fig. 1) together with sample sizes for females in parentheses.

The Foreman's group of three very small islands (0.17–0.36 ha) is of particular interest not only because of the apparent absence of melanics on Foreman's Island and their scarcity on Peashopper Island (2 of 273 females; number 1) but also because *P. spumarius* was absent from Crow's Island (27). These islands had small patches of similar vegetation to Ragged Island. The density of *P. spumarius* was extremely high on Foreman's, and high on Peashopper. The population samples were homogeneous in each sex (P is NS) and the TYP specimens were very pale in each sample in comparison to those from most other islands. The similarity of the populations on the two islands and their heterogeneity with that of the neighbouring large island (see below) suggests that one of them is likely to have been founded by a sizeable group from the other.

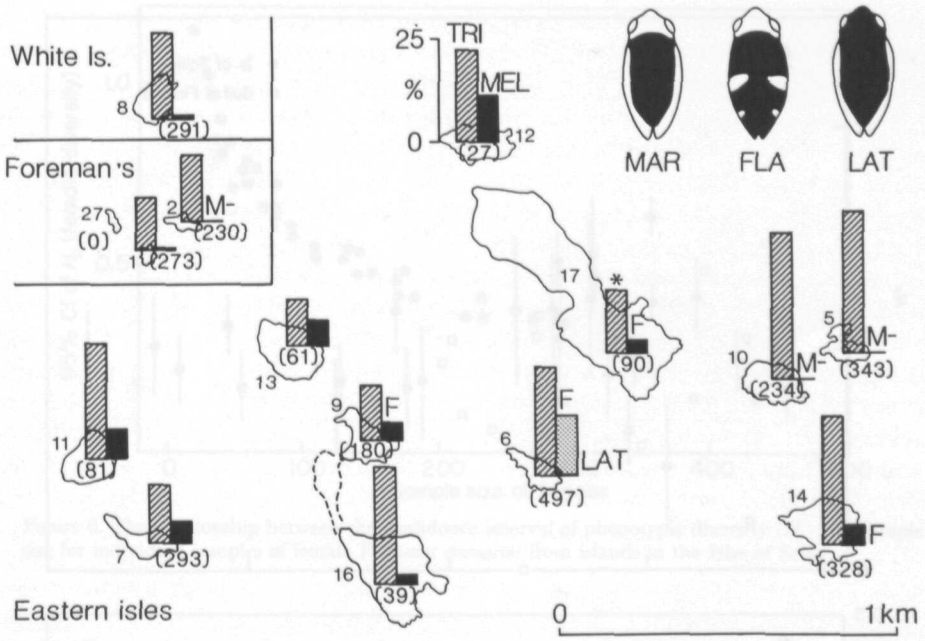

Figure 4. Frequency of *trilineatus* (TRI = hatched bars) and melanics (MEL = solid or stippled bars) in samples of female *Philaenus spumarius* from isolated islands smaller than 5 ha in the Isles of Scilly (*, larger island). The remainder of the samples are pale non-melanics (TYP + POP). Most melanics were the *marginellus* (MAR) form. F = presence of *flavicollis* (FLA) melanics; LAT + stippling = *lateralis* melanics; M- = no melanics. Map numbers are given (see Fig. 1) together with sample sizes for females in parentheses.

Figure 4 includes all the small, isolated islands which were sampled. Three other small islands were also visited which are connected to the largest island, St Mary's, by short sandy or rocky spits of land at low tide. One of these, Newford Island (4), yielded a sample which differed markedly from the combined sample from St Mary's (females: $\chi^2 = 18.46$, d.f. = 2; males: $\chi^2 = 13.22$, d.f. = 1 with $P < 0.001$ in each case). It was characterized by an extremely low frequency of *trilineatus*. Similarly the combined samples from Foreman's and Peashopper and that from White Island (8) differed from nearby large islands (females: $\chi^2 = 11.76$, d.f. = 2, $P < 0.01$ and $\chi^2 = 9.07$, d.f. = 2, $P < 0.05$, respectively; males: $P < 0.05$ and NS, see Figs 1 & 4). These results illustrate how small islands which are close to large islands may nevertheless differ from them in phenotype frequencies.

Patterns of diversity among islands

Figure 5 plots the indices of phenotypic and genic diversity within female populations against island area. Each index, including equitability and those for males (not shown), behaves in a closely similar manner, although they are not independent measures (e.g. $H_p \times H_g$: females, $r = 0.89$; males, $r = 0.84$ with $P < 0.001$). They show a similar comet-shaped distribution to that of the phenotype classes. The largest islands support populations of similar diversity whereas among the smaller islands, some populations are apparently less diverse

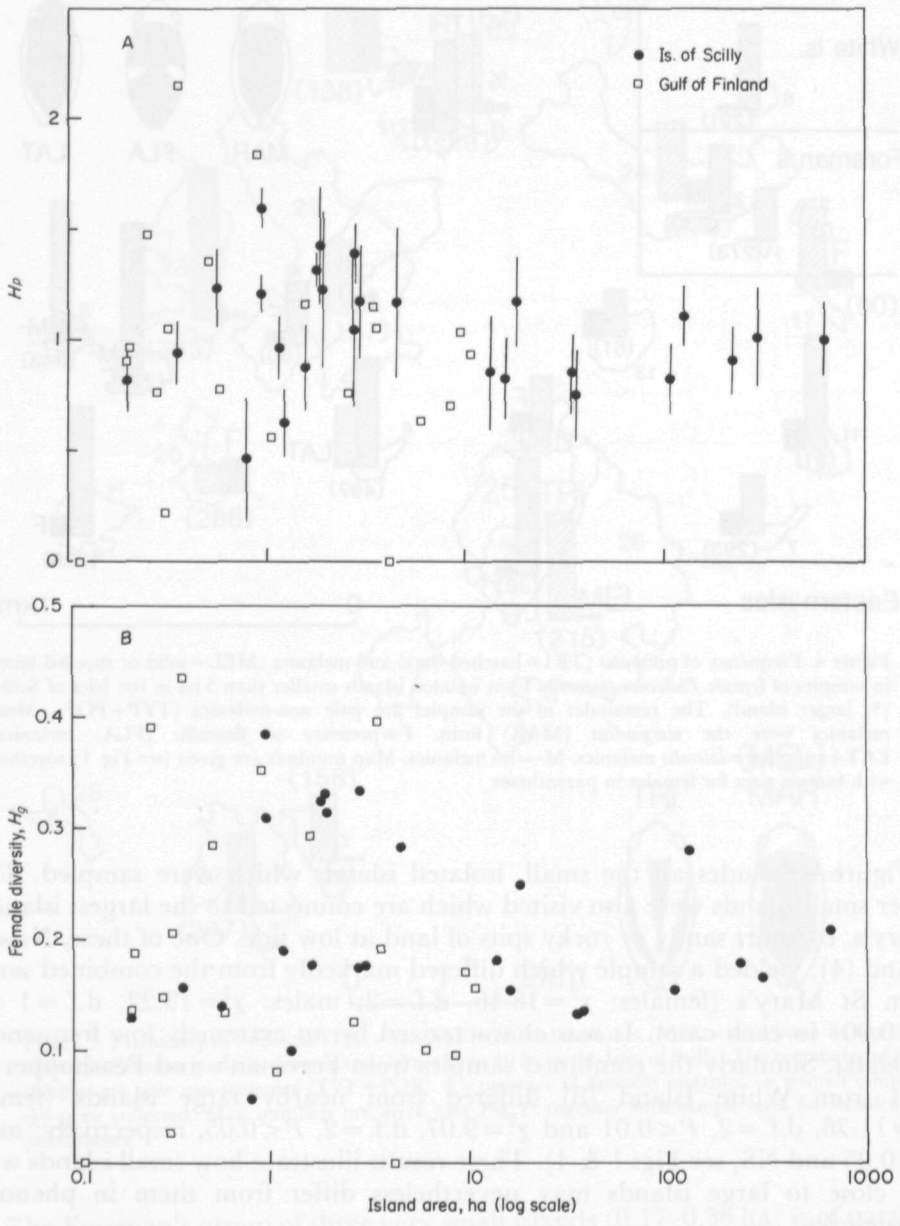

Figure 5. A, Phenotypic diversity (H_p) and B, genic diversity (H_g) in samples of female *Philaenus spumarius* plotted against island area for the Isles of Scilly and for the Gulf of Finland (data from Halkka *et al.*, 1970). Bars in A indicate $\pm$ twice the square root of the estimated variance (CI, see text) for samples from the Isles of Scilly.

while others are of similar, or greater diversity. The variance in female diversity is significantly greater among the sixteen islands smaller than 5 ha than among the ten islands larger than 10 ha (H_p: $F=4.81$; H_g: $F=4.21$ with $P<0.05$ for each value, 2-tail or 1-tail tests). However, there is a tendency for sample size to vary more among the smaller islands which were associated with greater extremes in population density in comparison to generally moderate densities on the largest

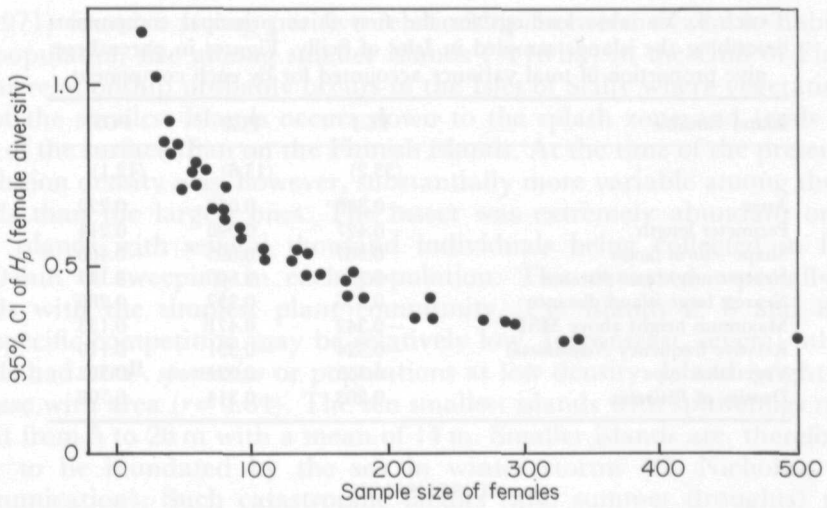

Figure 6. The relationship between the confidence interval of phenotypic diversity (H_p) and sample size for individual samples of female *Philaenus spumarius* from islands in the Isles of Scilly.

islands. Thus the comet-shaped distribution could be a sampling artifact rather than a real effect.

This problem was examined by applying a bootstrapping technique (Felsenstein, 1985) to examine how the 95% confidence limits (CLs) for the diversity indices in each sex vary with sample size. The procedure was: (1) to set up in a microcomputer a total Isles of Scilly 'population' equivalent to the numbers of individual phenotypes collected on all islands; (2) taking the observed sample sizes (N) in turn for each island, to 'sample the population' at random with replacement until N is reached; (3) to calculate diversity indices for that run and store; (4) after 1000 runs to take the 26th and 975th ranked values as the CLs for that island sample.

Figure 6 illustrates how the 95% confidence interval (CI) is highly dependent on sample size. However, the CIs show no coincidence in pattern with the comet-shaped distributions of the observed diversity indices (see also Fig. 5A for the variances calculated directly from the phenotype frequencies). This is emphasized by the lack of any correlation between the 95% CI and the absolute differences between observed diversity values and the overall mean (female H_p: $r=-0.07$; female H_g: $r=0.02$). Thus, populations which are extreme in diversity are not associated with relatively wide confidence limits.

Table 4 gives the factor weightings from a principal component analysis performed on the island variables. There are high intercorrelations between variables and the first principal component accounting for 53% of the total variance is closely related to island area ($r=0.88$). This component also shows a similar comet-shaped distribution when plotted against diversity indices (Fig. 7). Later components show no clear relationships. The lack of additional explanatory power provided by the other independent variables is emphasized by the failure of a canonical correlation analysis involving this set of variables and the frequency data for alleles or phenotypes to provide correlations which can be interpreted biologically.

TABLE 4. Variable loadings for the first three principal components describing the islands sampled in Isles of Scilly. Figures in parentheses give proportion of total variance accounted for by each component

Island variable	PC1	PC2	PC3
	(53.2)	(13.6)	(12.1)
Area	−0.388	0.052	0.222
Perimeter length	−0.427	0.098	0.214
Shape—form factor	0.307	−0.095	−0.408
Nearest neighbour distance	0.268	0.600	0.147
Nearest large island distance	0.336	0.357	0.286
Maximum height above MSL	−0.342	0.471	0.153
Relative frequency *Neophilaenus*	−0.324	−0.351	0.119
Vegetation type	−0.355	0.221	−0.323
Density of *Philaenus*	0.203	−0.314	0.702

DISCUSSION

Population history, drift and diversity

What processes are the basis of the observed patterns of within and between-island population variation? Before this question can be examined it is necessary to consider a scenario for the population dynamics of *P. spumarius* on large and small islands. Since the break-up of the original land mass into the present-day archipelago, populations of spittlebugs have probably occurred continuously on the larger islands. The sub-populations on the larger islands sampled in the present study tended to be at a fairly uniform and moderate density. Total population sizes must be very large and are likely to be relatively stable. In contrast, populations on the smallest islands are probably subject to extinction-recolonization cycles and extremes in fluctuations of population size. Halkka *et*

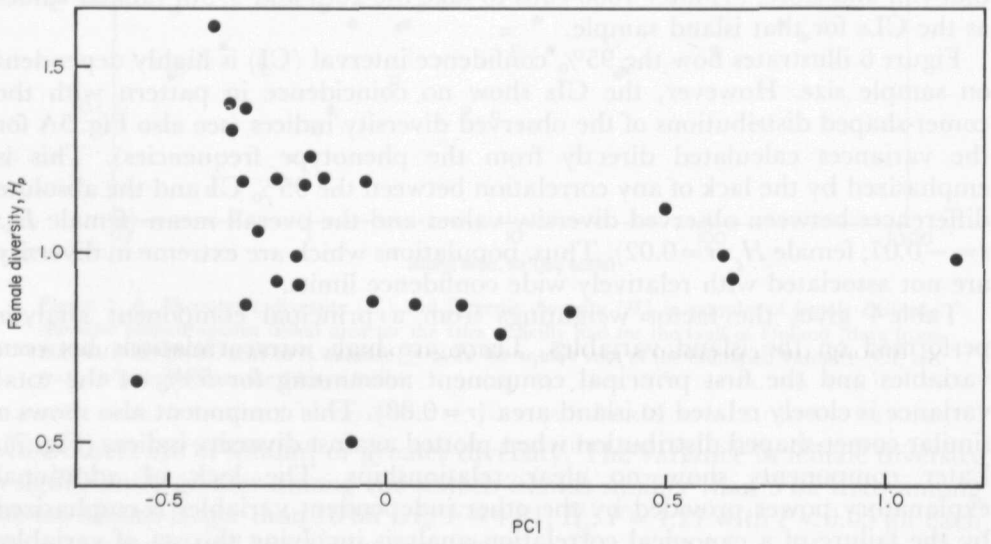

Figure 7. Phenotypic diversity (H_p) in samples of female *Philaenus spumarius* from the Isles of Scilly plotted against the first principal component for the independent variables describing island size, isolation and ecology.

al. (1971) found a strong positive relationship between available habitat area and population size among smaller islands (<10 ha) in the Gulf of Finland. A similar relationship probably occurs in the Isles of Scilly where vegetation on all except the smallest islands occurs down to the splash zone and tends to cover more of the surface than on the Finnish islands. At the time of the present survey population density was, however, substantially more variable among the smaller islands than the largest ones. The insect was extremely abundant on several small islands with several thousand individuals being collected in less than 15–30 min of sweeping in each population. This occurred especially among islands with the simplest plant community (e.g. islands 2, 6 and 8) where interspecific competition may be relatively low. In contrast, several other small islands had no *P. spumarius* or populations at low density. Island height tends to increase with area ($r=0.64$). The ten smallest islands with spittlebugs ranged in height from 5 to 26 m with a mean of 14 m. Smaller islands are, therefore, more likely to be inundated by the sea in winter storms (C. Nicholas, personal communication). Such catastrophic factors (also summer droughts) probably lead to intermittent population crashes (bottlenecks) and colonization-recolonization cycles. On many, although probably not all, islands there is likely to be a rapid increase in numbers after a successful colonization due to a high intrinsic rate of increase and 'ecological release'. This form of population dynamics will tend to decrease stochastic changes in heterozygosity over a bottleneck (Nei, Maruyama & Chakraborty, 1975; Janson, 1987). The Isles of Scilly can probably be represented as a discrete metapopulation within which sub-populations vary in how transient they are. The populations of the largest islands probably represent more or less stable 'migrant-pools' while those of the smallest islands, depending on their degree of exposure to the effects of extreme weather, are rather transient and unstable. The situation is likely to be similar to the metapopulation of the butterfly *Euphydryas editha* studied by Harrison, Murphy & Ehrlich (1988), although direct information on population dynamics is lacking.

The significant variation between island populations, including in many cases close neighbours, argues that rates of gene flow are low. This is supported further by the observations of the Foreman's group of three very small islands. *Philaenus spumarius* was absent on Crow's Island in spite of its similar vegetation and close proximity to the other two islands, suggesting that islands are only colonized at a low rate. It is noteworthy that Crow's Island is the lowest (height = 5 m) sampled in the Isles of Scilly and, therefore, is more likely than most others to be inundated by winter storms. Halkka *et al.* (1971) conclude that active movement of adult spittlebugs by flight is probably limited to distances of about 40 to 80 m. This upper limit corresponds to the shortest distances between isolated islands (e.g. among the Foreman's group) although passive wind transport may occur over longer distances (Weaver & King, 1954). Halkka *et al.* (1971, 1974) consider that most inter-island dispersal in the Gulf of Finland with its brackish water occurs by dislodgement through strong winds followed by surface-drifting (as demonstrated experimentally). However, this is much less likely in the Isles of Scilly because of the high salinity of the seawater (A. Saura, personal communication).

The phenotypic and genetic characteristics of the large island populations are similar to populations in southern England (Lees, Dent & Gait, 1983). They are

probably influenced by a regime of visual and climatic selection broadly similar to that influencing the colour polymorphism in such mainland populations. A wide variety of such selective influences have been postulated or received some empirical support (Owen & Weigert, 1962; Thompson, 1973, 1984; Harper & Whittaker, 1976; Halkka & Mikkola, 1977; Halkka *et al.*, 1979; Lees *et al.*, 1983; Berry & Willmer, 1986).

In contrast, the greater dispersion of measures of diversity among the smaller islands, which yields comet-shaped distributions in plots against island area, is consistent with a major influence of random genetic drift associated with founder events or bottlenecks in population size. There are no clear relationships between diversity indices and either spittlebug densities or vegetation type arguing against an alternative selection-based hypothesis similar to that invoked in *Maniola jurtina* (Ford, 1975). The *t* and *T* alleles occur in all populations but the less frequent melanic *M* allele is probably absent in some small island populations although it occurs on all larger islands. Each allele is more variable in frequency among the smaller islands. Evidently drift leading to increases in frequencies of alleles other than *t* on *some* smaller islands leads to greater evenness of allele frequencies and higher diversity measures in these populations. On the other hand, a few islands show the loss of the rare melanic alleles, and others have lowered frequencies of *T*, reducing diversity.

There is no indication of overall loss of heterozygosity within the populations on smaller islands (see Table 3 and Fig. 5). Substantial declines in average heterozygosity are only expected with extreme bottlenecks. In contrast, the variance of average heterozygosity among populations is more sensitive to sampling effects (see Fig. 6). This difference in sensitivity is illustrated further by running the bootstrapping simulations described above for a wide range of 'population sizes' (Brakefield, 1989). Loss of melanics (rare alleles) from some populations on smaller islands and a substantially increased variance among these populations with little overall loss of average heterozygosity is expected with single-generation bottleneck effects or founder events equivalent to a few tens of individuals.

Distribution of melanic alleles among islands

Examination of the phenotype frequency data from the Isles of Scilly with regard to genetical studies by Halkka *et al.* (1973) and Stewart & Lees (1988) shows that *marginellus* females were the heterozygote *M*/*t* perhaps with a few homozygote *M*/*M*. The genotype *F*/*L* also produces the MAR phenotype through codominance of the alleles controlling FLA and LAT. However, the *L* allele was apparently only present on Ragged Island. The single MAR female from Ragged Island may have been of the genotype *F*/*L*; a single female was also collected with the *flavicollis* phenotype combined with the white border of MAR and LAT (see Fig. 4). The latter MAR-FLA individual was probably an *M*/*F* heterozygote. LAT differs from MAR in having a black, rather than a white head (Fig. 4). It is at a higher frequency on Ragged Island than in other populations sampled throughout the extensive range of the species except for several island populations in the Gulf of Finland (Halkka *et al.*, 1970). The most likely explanation for this high frequency, in the light of the absence of *L* on other islands, is the occurrence of a mutation very early in the (last) colonization

of Ragged Island or possibly during a bottleneck. An origin during a period of very small population size producing an initially high frequency would greatly increase the chance of LAT attaining its present-day substantial frequency in a large population. There has probably also been some increase in allele frequency by drift since the original mutation. Halkka *et al.* (1973) suggest that the colour locus in *P. spumarius* may be a supergene and that the *M* allele was produced by duplication in an L/C heterozygote. Following from this idea, the *L* allele on Ragged Island may have arisen through unequal crossing-over in a MAR individual. Crosses with LAT material from mainland Britain could determine whether the similar phenotypes have the same genetic basis.

Thus the occurrence of *L* at high frequency on Ragged Island seems to be a particularly interesting example of stochastic effects on the smaller islands. Of course it is possible that LAT is at some selective advantage on this island thus accounting, at least in part, for any increase in frequency since its origin. This is unlikely to involve a thermal advantage because of the high summer levels of insolation in the Isles of Scilly, although periods of morning mists are also common. Similarly visual selection appears unlikely because of the very small size of the island and the probable absence of insectivorous birds or small mammals, except perhaps in the former case as transitory individuals.

The *C* allele controls a FLA phenotype and two other melanic phenotypes with white heads in females (GIB and LCE). This allele may be absent in the Isles of Scilly archipelago since no GIB or LCE females were collected and the single male scored as LCE may have been LOP (see Stewart & Lees, 1988). The LOP, QUA and ALB phenotypes are controlled by the *O* allele which is present at a very low frequency in the Isles of Scilly (see Appendix). Thus six of the seven alleles at the colour locus are probably present in the Isles of Scilly.

The proportion of total diversity accounted for by between-island diversity is less than 5% even for the smallest islands (Table 3). Wool (1987) tabulates the results of some comparable studies of island populations although these usually involved larger and more widely-spaced islands. The values for *P. spumarius* are similar to the lowest class of comparable values tabulated by Wool which represented variation at some polymorphic enzyme loci in *Drosophila*.

Comparison with islands in the Gulf of Finland

The results of the present study can be compared with those of O. Halkka and his co-workers from islands in the Gulf of Finland (Halkka *et al.*, 1970). The Finnish islands are of similar age and nature to those in the Isles of Scilly although they were created by uplifting rather than submergence. The values of phenotypic and genic diversity calculated for 21 island populations sampled by Halkka and his co-workers in 1969 (minimum sample size = 25 females) are plotted in Fig. 5 together with those for the Isles of Scilly. There appears to be a similar comet-shaped distribution against island area although it is somewhat truncated by the absence of large islands. Some caution is necessary in interpreting these data since application of the bootstrapping procedure shows that, unlike for the Isles of Scilly, extremes in diversity indices are associated with wider confidence limits (female H_p: $r = 0.50$, $P < 0.05$; female H_g: $r = 0.71$, $P < 0.001$).

There are comparatively many more islands of less than 1 ha among the

Finnish islands. These show a very wide dispersion of diversity measures which tends to extend beyond the distribution for the Isles of Scilly (Fig. 5). The Finnish islands vary much more in their degree of isolation than those in the Isles of Scilly with many lying close to the coast while three others are 10–12 km from the mainland. One of the latter islands (4 ha in area) yielded 115 females and 104 males which were all TYP indicating fixation of the *t* allele presumably as the result of strong stochastic effects. Saura, Halkka & Lokki (1973) also examined variation at 20 enzyme loci in a mainland population and six of the island populations. Their results are also consistent with increasing effects of genetic drift in smaller and more isolated populations. Halkka *et al.* (1970, 1971, 1974) argue that both processes of selection and of genetic drift strongly influence the colour polymorphism in island populations. A later assessment (Halkka *et al.*, 1976) placed more emphasis on selection. The temporal stability of some populations and transplantation and perturbation experiments provide evidence for a contribution to population differentiation of selection to specific environments (Halkka *et al.*, 1974, 1975, 1976). Selection may also be important among smaller islands in the Isles of Scilly but without studies of temporal variation or the use of transplantation and perturbation experiments it will be impossible to conclude one way or the other. At present the observations are consistent with a major role for founder effects and genetic drift during periods of small population size which act to produce some loss of rare alleles and a wider range in diversity measures among smaller islands than in populations on large islands.

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APPENDIX

Phenotype frequencies in samples of *Philaenus spumarius* from islands in the Isles of Scilly. Frequencies for males and females are given on the upper and lower lines, respectively

Map No./ island	Island area (ha)	Phenotype											
		POP	TYP	TRI	Other N.M.	MAR	LAT	FLA	LCE	QUA	ALB	LOP	MAR-FLA
1.	0.20	60	272	115									
Peashopper		9	227	35		2							
2.	0.36	94	234	87									
Foreman's Is.		13	179	38									
3.	0.57	28	338	99						2			
Taylor's Is.		30	157	29	1	1				1			
4.	0.81	2	97	8									
Newford Is.		1	80	2		3							
5.	0.95	54	249	188									
Little Innisvouls		19	205	119									
6.	0.96	65	376	204									
Ragged Is.		17	274	132		1	72						1
7.	1.16	17	385	84							1		
Little Ganinick		3	232	42		16							
8.	1.27	12	305	33									
White Is.		3	258	25		5							
9.	1.60	6	177	25				1					
Little Arthur			147	25		5		3					
10.	1.81	47	134	87									
Great Innisvouls		20	128	86									
11.	1.89	4	67	23									
Great Ganinick		2	50	23		2		4					
12.	1.93	2	23	1									
Nornour			18	6		3							

13.	2.79	13	62	13								
Little Ganilly		2	48	7		4						
14.	2.83	62	302	191			1	1				
Menawethan		10	198	103		13	2		2			
15.	3.00	7	240	33								
Toll's Is.		6	114	16	6	5						
16.	4.63	6	42	19								
Great Arthur		1	26	11		1	1					
17.	13.64	1	102	26								
Great Ganilly			73	14		1	2					
18.	16.20	1	135	25								
Tean		3	137	25		2						
19.	18.43	2	128	30								
St Helen's			102	17	3	16						
20.	35.50	3	272	21						1		
Sampson		1	246	16	4	14	4		1			
21.	36.83	5	182	38								
Gugh		2	132	20	1	1						
22.	109.55		259	56								
St Agnes		5	202	38	1	1						
23.	129.69	4	245	106								
Bryher		5	151	66		3						
24.	228.31	3	281	55								
St Martin's		2	225	42		8	2					
25.	301.06	3	138	27								
Tresco		5	125	21		5					1	
26.	662.06	7	257	81								
St Mary's		5	162	45	1	2						

Island 27 = Crow's Island; 28 = Annet; 29 = White Island (off St Martin's). Abbreviations of phenotypes: *populi* (POP); *typicus* (TYP); *trilineatus* (TRI); *marginellus* (MAR); *lateralis* (LAT); *flavicollis* (FLA); *leucocephalus* (LCE); *quadrimaculatus* (QUA); *albomaculatus* (ALB); *leucophthalmus* (LOP).

Other N.M. = non-melanics other than POP, TYP and TRI. They were similar to *praeusta* but with varying expression of dark lattice-like markings posteriorly on the elytra (cf. *ustulata* without the black head and anterior elytra).