The variance in genetic diversity among subpopulations is more sensitive to founder effects and bottlenecks than is the mean: A case study

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Evolutionary Biology of Transient Unstable Populations

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The Variance in Genetic Diversity Among Subpopulations is More Sensitive to Founder Effects and Bottlenecks Than is the Mean: A Case Study

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Introduction

There are three widely-recognised effects of genetic drift on polymorphic traits which are associated with 'bottlenecks' or 'founder events' in populations. Rare alleles are expected to be lost, average heterozygosity to decline, and the variance among populations to increase. The theoretical work is summarized in Nei (1987). These effects have been documented many times in laboratory populations (e.g. Buri, 1956; Dobzhansky and Pavlovsky, 1957; Rich, Bell and Wilson, 1979; Wool, 1987). Information from natural populations is less extensive and has often involved allozyme variation, especially on islands or in newly-colonized mainland areas (e.g. Janson, 1987; Black et al., 1988; work cited in Wool, 1987). Most studies have, however, tended to concentrate either on the description of the loss of heterozygosity or rare alleles within populations, or on the increase in differentiation among populations. Moreover, many studies involving polymorphic enzyme loci tend to be based on comparatively small samples so that there is uncertainty about whether rare alleles are present or not in populations thought to have experienced genetic drift.

This paper explores the relative contributions of the effects of genetic drift to changes in phenotypic and genetic diversity within and among populations in relation to founder events or bottlenecks of varying magnitude. Data for a homopteran insect which describe the frequencies of melanic phenotypes controlled by a polymorphic gene in large samples from an island archilepago are analysed and used as the basis for a series of simple simulations. The island populations appear to conform to a type of metapopulation structure (Levins, 1970; Harrison, Murphy and Ehrlich, 1988; Wade and McCauley, 1988) with rates of extinction and recolonization, and of inter-population migration probably varying between islands in relation to their size and height. The results reproduce the well-known finding that substantial genetic diversity at polymorphic gene loci only tends to be lost in association with more extreme founder events or population bottlenecks. In contrast, the variance in diversity among populations is much more sensitive to genetic drift.

The island archipelago and collection of samples

The meadow spittlebug Philaenus spumarius is a rather sedentary insect which is abundant in many grassland habitats in Europe. It is common in the Isles of Scilly about 40 km off the southwest coast of England (Fig. 1). In July 1986 vegetation was swept with a stout net on twenty-nine islands

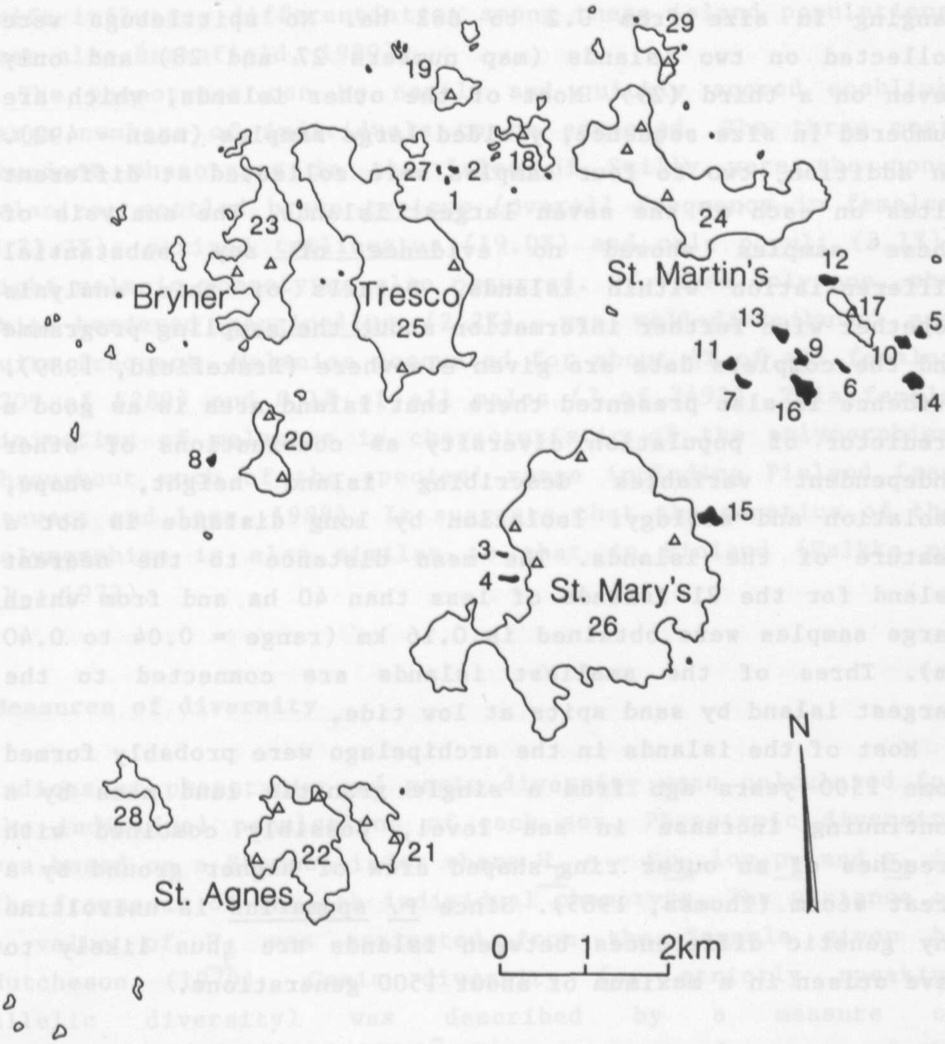

Fig. 1. Map of the Isles of Scilly. All islands which were visited are numbered with those of less than 5 ha in black. Triangles show sampling sites on islands of more than 10 ha

ranging in size from 0.2 to 662 ha. No spittlebugs were collected on two islands (map numbers 27 and 28) and only seven on a third (29). Most of the other islands, which are numbered in size sequence, yielded large samples (mean = 492). In addition, two to four samples were collected at different sites on each of the seven largest islands. The analysis of these samples showed no evidence of any substantial differentiation within islands. Details of this analysis together with further information about the sampling programme and the complete data are given elsewhere (Brakefield, 1989). Evidence is also presented there that island area is as good a predictor of population diversity as combinations of other independent variables describing island height, shape, isolation and ecology. Isolation by long distance is not a feature of the islands. The mean distance to the nearest island for the 21 islands of less than 40 ha and from which large samples were obtained is 0.16 km (range = 0.04 to 0.40 km). Three of the smallest islands are connected to the largest island by sand spits at low tide.

Most of the islands in the archipelago 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 a maximum of about 1500 generations.

The study organism and the polymorphism

Philaenus spumarius is polymorphic for eleven widely-distributed non-melanic and melanic phenotypes (see illustrations in Halkka et al., 1973). The polymorphism has been investigated extensively in natural populations including those on small islands in the Gulf of Finland. Halkka et al., (1970, 1974, 1976) concluded that both selection and genetic drift influence differentiation among these island populations (see also Brakefield, 1989).

The phenotypes can be easily and quickly scored enabling large numbers of individuals to be screened. The three most abundant phenotypes in the Isles of Scilly were the non-melanics: mottled brown typicus (overall frequency in females = 73.7%), striped trilineatus (19.0%) and pale populi (3.1%). Eight melanic phenotypes also occurred. Of these only one, the white-bordered marginellus (2.2%), was well-distributed and quite frequent. Melanics accounted for about 4% of all females (209 of 5289) and 0.1% of all males (7 of 7492). This female limitation of melanics is characteristic of the polymorphism throughout much of the species' range including Finland (see Stewart and Lees, 1988). It suggests that the genetics of the polymorphism is also similar to that in Finland (Halkka et al., 1973).

Measures of diversity

Indices of phenotypic and genic diversity were calculated for the individual populations of each sex. Phenotypic diversity was 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. The variance of a value of H_p was estimated from the formula given by Hutcheson (1970). Genic diversity (or strictly speaking allelic diversity) was described by a measure of heterozygosity, $H_g = 1 - \Sigma a_i^2$ where a_i is the frequency of the ith allele. The following assumptions which are based on the breeding studies of Halkka et al., (1973) and Stewart and Lees (1988) were used to infer allele frequencies from the data for phenotype frequencies: (1) the top dominant T allele in each sex controls the trilineatus phenotype; (2) melanic phenotypes are controlled by a single Me allele of intermediate dominance in females and recessive in males (there may also be reduced penetrance) and (3) the typicus and populi phenotypes are controlled (principally) by the t allele which is recessive in females and of intermediate dominance in males. 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* form controlled by the M allele (one of several melanic alleles which have been identified). Estimation of allele frequencies then assumes that populations are in Hardy-Weinberg equilibrium. For the entire sample the estimated allele frequencies are T = 0.1016, Me = 0.0223 and t = 0.8761 in females and T = 0.0883, me = 0.0306 and t = 0.8812 in males.

Average heterozygosity and the distribution of rare alleles

If the islands are grouped into five classes with respect to area there is no indication of any decrease in average heterozygosity with declining size (Table 1).

Melanics were collected on all islands except three of the smallest: islands 2 (0.36 ha), 5 (0.95 ha) and 10 (1.81 ha); the last two being close neighbours (see Fig. 1). The large sample sizes concerned in these cases (230 to 343 females) suggest that melanic alleles were absent in each population. For example, combining across islands 5 and 10 and applying the binomial distribution, the predicted phenotype frequency at which there would have been a greater than 95% chance of collecting at least one melanic female is 0.55% (see also Fig.

Table 1. The mean values of the indices of phenotypic (H_p) and genic (H_g) diversity for samples of *Philaenus spumarius* from islands grouped by area. The number of islands is given in parentheses

Diversity index	Island area, ha				
	0-1 (6)	1-2 (6)	2-5 (4)	10-40 (5)	100-700 (5)
Female H_p	1.0417	1.0710	1.1984	0.8954	0.9740
Female H_g	0.1972	0.2405	0.2431	0.1717	0.1987
Male H_p	1.1746	0.9059	1.1254	0.7074	0.8061
Male H_g	0.2226	0.1562	0.2067	0.1501	0.1938

2A). The *marginellus* form, and therefore the M allele, was present on all the 23 islands where melanics were found.

Patterns of diversity against island area

Figure 2 plots the indices of phenotypic and genic diversity within female populations against island area. The scatters show similar comet-shaped distributions. Those for males and for the major phenotypes show similar patterns (Brakefield, 1989). The two diversity indices are closely correlated (*r* = 0.89) and not independent. The scatter plots suggest that the largest islands support populations of similar diversity at this polymorphic locus whereas there is increased variance among the smaller islands. A corresponding analysis of genic diversity (Nei, 1987) shows that differentiation between islands accounts for about 3-4 times more of total diversity for the smaller, than the larger islands (Table 2). However, the fraction of between-population variation is consistently less than 5%. Chi-square analyses of the frequency distributions of phenotypes show that significant heterogen-

Table 2. Analysis of genic diversity in the populations of *Philaenus spumarius* grouped by island area

Island area (ha)	Females			Males		
	H_T	H_S	G_{ST}	H_T	H_S	G_{ST}
0.2-1	0.2070	0.1972	0.0471	0.2287	0.2226	0.0264
1-2	0.2474	0.2405	0.0277	0.1619	0.1562	0.0348
2-5	0.2476	0.2431	0.0184	0.2124	0.2067	0.0270
10-40	0.1731	0.1717	0.0083	0.1513	0.1501	0.0078
100-700	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

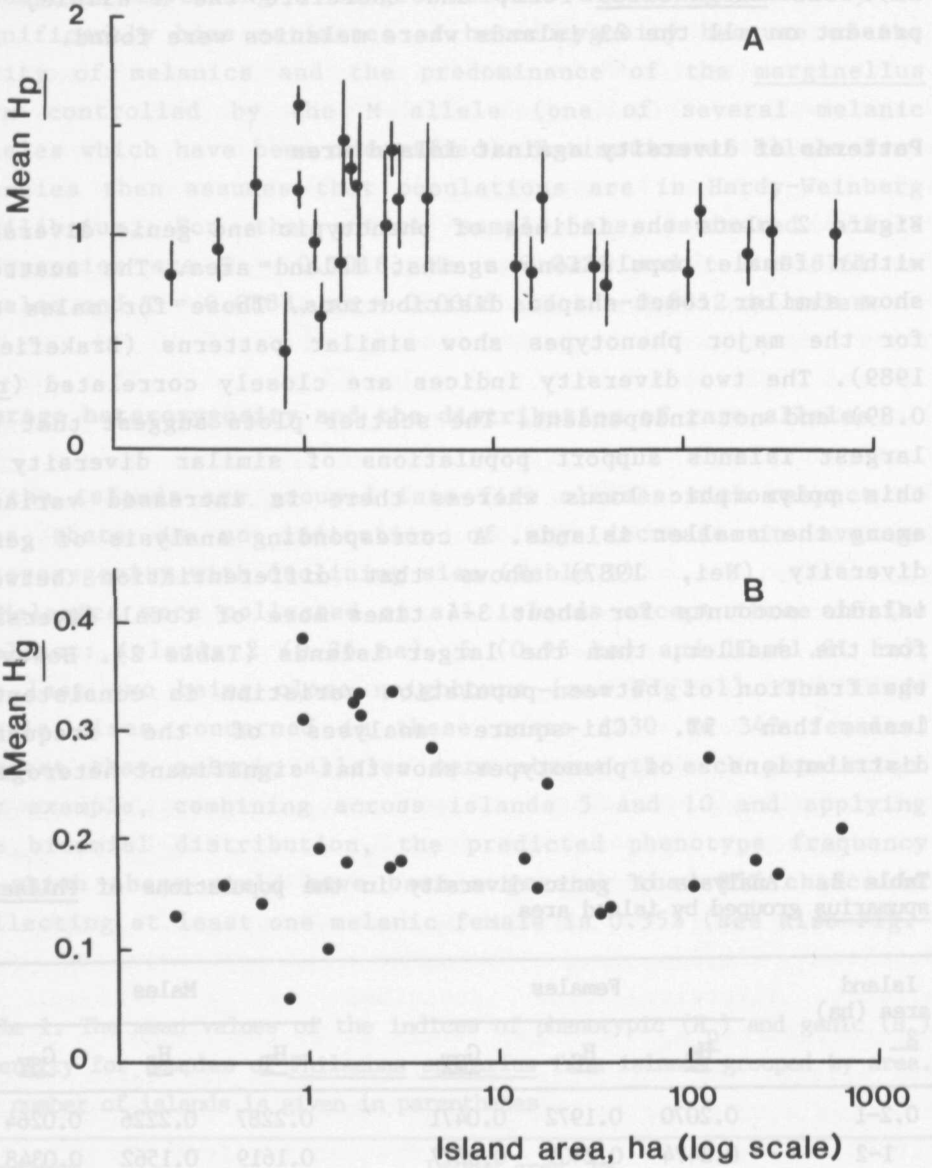

Fig. 2. A. Phenotypic diversity (Hp) and B. Genic diversity (Hg) in samples of female *Philaenus spumarius* plotted against island area. Bars in A. indicate ± twice the square root of the estimated variance (see text)

eity occurs among populations within each of the five classes of island area (Brakefield, 1989; see also Fig. 2A).

Effects of sample size on diversity indices

The apparent increase in variance among populations on small islands could be an artefact of greater variability in sample size. A bootstrapping procedure was used to examine this possibility by estimating the 95% confidence limits (CLs) for each value of the diversity indices for populations of females. The procedure was: (1) to set up in a microcomputer an Isles of Scilly 'metapopulation' equivalent to the total numbers of females collected of the individual phenotypes; (2) taking the observed sample sizes for females (N) in turn for each island, to 'sample the metapopulation' 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.

There is no correlation between the range of the upper and lower confidence limits and the absolute difference between the observed value for diversity and the overall mean (female $\underline{H_p}$: $\underline{r}$ = -0.07; female $\underline{H_g}$, $\underline{r}$ = 0.02). This also holds when the calculated estimates of the variance of the observed values of phenotypic diversity are examined ($\underline{r}$ = -0.11; see Fig. 2A). Thus, populations which are extreme in diversity are not associated with relatively wide confidence limits and the increased variance among populations on small islands is not an artefact of sample size.

Expected relationships between founder effects and diversity

The bootstrapping procedure was also used to examine the expected relationships between sampling error and the statistics describing diversity at the melanic locus in the Isles of Scilly. Instead of using the observed sample sizes for islands in the simulations, a sequence of sets of 1000 single-generation samples or 'populations' of increasing size (N) was generated. The mean values of diversity and the confidence limits for the diversity indices then represent those expected for populations at the point of a founder event or bottleneck of magnitude given by the different values of N. There are clearly severe limitations in this procedure with respect to simulating the real stochastic processes influencing differentiation in the Isles of Scilly. In at least some cases involving the establishment of a population, colonizers will arrive in several 'waves'. The effects of population history will not be represented at all faithfully by single-generation sampling: they also depend on the time elapsed since the sampling event, on the duration of the bottleneck and the subsequent rate of population increase (Nei et al., 1975, Janson, 1987). Variation in population size between islands and migration between extant populations are also not taken into account. With respect to founder events, the simulations are based on a pure "migrant pool" model where the N colonists are a random sample from the entire (meta)population. A more realistic approach would involve migration assortative by distance. In this case colonists at a particular location are a mix of individuals drawn in some weighted-by-distance way from a few nearby populations. In a "propagule model", the colonists (2N gametes) would come from a single randomly chosen local population. However, there is no information about how the potential source populations should be weighted by distance. Wade and McCauley (1988) examine for a meta-population how the amount of differentiation and the genetic effects of colonization and extinction depend critically upon the applicability of such models and on the relative magnitudes of the number of colonists and the number of migrants moving between extant populations.

Within these types of limitations, the simulations clearly show that in general the confidence limits for measures of diversity among populations are much more sensitive to sampling effects and genetic drift than are the mean values for diversity across populations (Figs 3 and 4). The effects

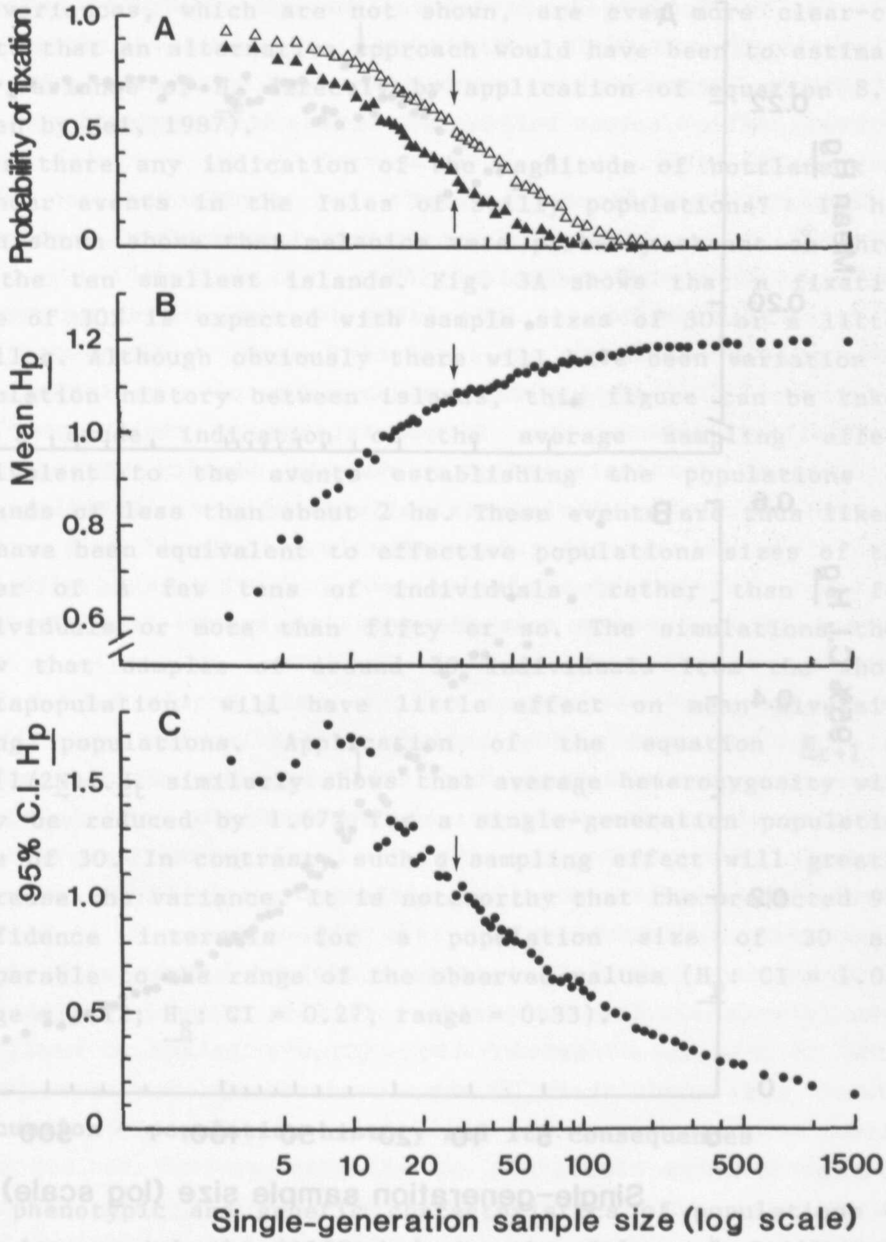

Fig. 3. The results of single-generation sampling effects of varying magnitude on phenotypic diversity as obtained from simulations (see text) using the total Isles of Scilly 'population' of females: A. Proportion of replicates with no melanics (▲) or none of the marginellus form (△); B. the mean phenotypic diversity ($\underline{H_p}$) and C. the 95% confidence interval of $\underline{H_p}$. Arrows indicate the sampling effect yielding a rate of fixation of non-melanics similar to that observed among the ten smallest islands

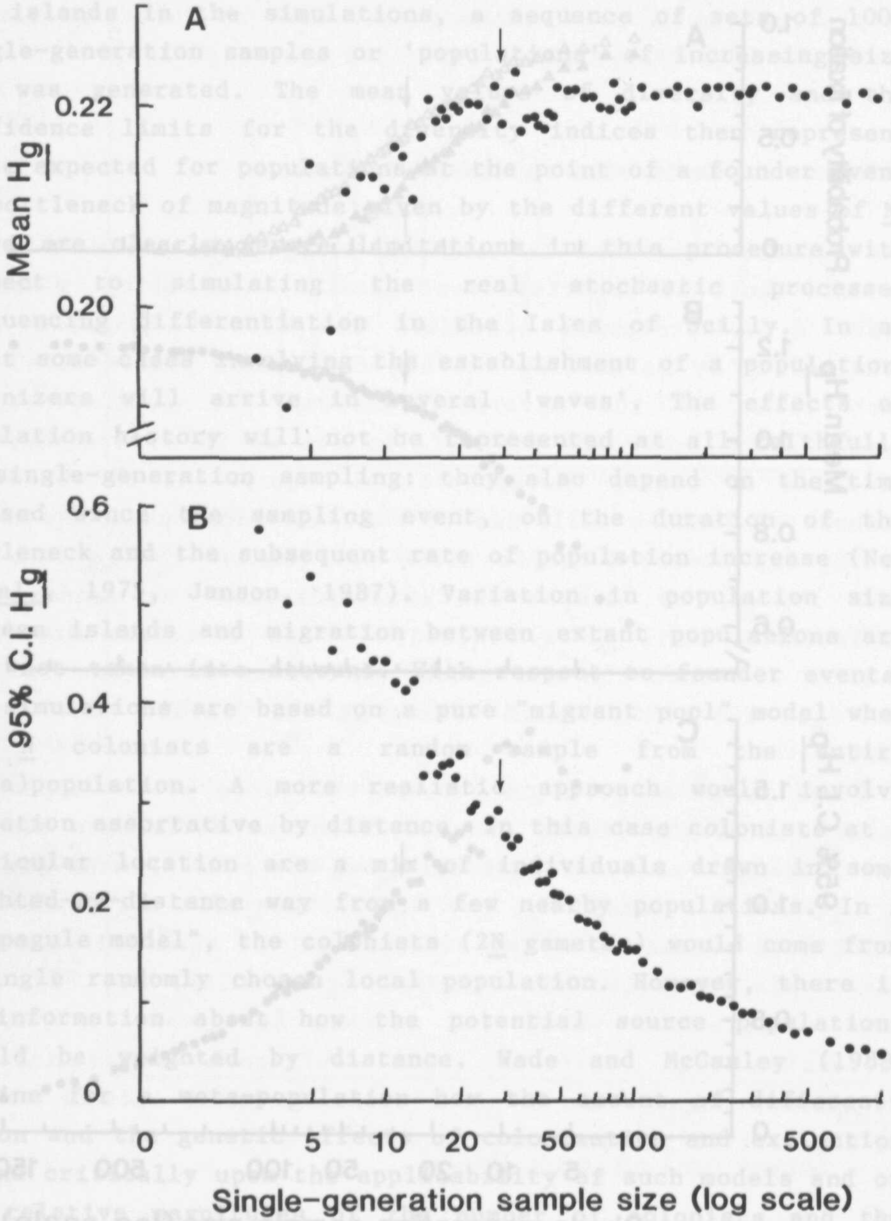

Fig. 4. The results of single-generation sampling effects of varying magnitude on genic diversity as obtained from simulations (see text) using the total Isles of Scilly 'population' of females: A. the mean genic diversity index (Hg) and B. the 95% confidence interval of Hg. Arrows indicate the magnitude of sampling effect yielding a rate of fixation similar to that observed among the smallest islands

on variances, which are not shown, are even more clear-cut (note that an alternative approach would have been to estimate the variance of $\underline{H}_g$ directly by application of equation 8.12 given by Nei, 1987).

Is there any indication of the magnitude of bottleneck or founder events in the Isles of Scilly populations? It has been shown above that melanics were probably absent on three of the ten smallest islands. Fig. 3A shows that a fixation rate of 30% is expected with sample sizes of 30 or a little smaller. Although obviously there will have been variation in population history between islands, this figure can be taken as a crude indication of the average sampling effect equivalent to the events establishing the populations on islands of less than about 2 ha. These events are thus likely to have been equivalent to effective populations sizes of the order of a few tens of individuals, rather than a few individuals or more than fifty or so. The simulations then show that samples of around 30 individuals from the whole 'metapopulation' will have little effect on mean diversity among populations. Application of the equation $\underline{H}_{t+1}$ = $[1-(1/2\underline{N})].\underline{H}_t$ similarly shows that average heterozygosity will only be reduced by 1.67% for a single-generation population size of 30. In contrast, such a sampling effect will greatly increase the variance. It is noteworthy that the predicted 95% confidence intervals for a population size of 30 are comparable to the range of the observed values ($\underline{H}_p$: CI = 1.05, range = 1.12; $\underline{H}_g$: CI = 0.27, range = 0.33).

Discussion - population history and its consequences

The phenotypic and genetic characteristics of populations on the larger islands (>100 ha) in the Isles of Scilly are similar to those on the mainland of southern England and they are probably influenced by a broadly similar regime of visual and climatic selection (Lees, Dent and Gait, 1983). The differentiation found among the populations of small islands after less than 1500 or so generations is consistent with a major influence of genetic drift. Although, there are no clear relationships between diversity and crude indices of spittlebug densities or vegetation type, selection may, of course, also have influenced the differentiation (see Brakefield, 1989).

Several observations suggest that populations on small islands are transient and experience intermittent population crashes (see also Brakefield, 1989):

1) Field observations of spittlebug density, including records of captures per sweep of standard length, suggest that the density of P. spumarius was substantially more variable among the smaller islands than in populations on the larger ones which were characterized by a moderate density. The density was low on some small islands while on others, including some with a very simple plant community (e.g. islands 2, 6 and 8), it was extremely high. Colonization of small islands with such an established plant community is likely to lead to rapid increases in population size.

2) P. spumarius was absent on the small Crow's Island (27). This was apparently due to an earlier extinction with no successful recolonization since the island was of similar size and habitat to two close neighbours where the spittlebug was abundant. The species was also not found on the intermediate-sized island of Annet (28) although not all the suitable vegetation was searched.

3) There is a trend of increasing island height with island area ($r = 0.64$). The ten smallest islands range in height from 5 to 26 m with a mean of 14 m (Crow's Island = 5 m). The lowest are more likely to be inundated by seawater during winter storms; a process which may well lead to population crashes or extinctions.

4) The melanic form lateralis controlled by the L allele (Halkka et al., 1973) was at a substantial frequency of 14.5% in females on the small Ragged Island (6). It was not found on any of the neighbouring group of 10 islands or in any other samples. It seems likely that the L allele arose as a mutant when this presently very large and high density population on Ragged Island was in an early phase of establishment or

passing through an extreme bottleneck. Alternatively the high frequency may indicate that this allele is favoured by selection: it would be interesting to introduce it elsewhere. The marginellus form was present at a very low frequency on Ragged Island (1 of 497 females).

Observations also suggest that the rate of migration between islands and of colonization is probably rather low. The case of Crow's Island which had not been colonized from two close neighbours is a case in point. If the polymorphism is not influenced by strong selection in response to variable environments on the small islands (cf. Ford, 1975), then the differentiation which frequently occurs between closely neighbouring islands (including those joined at low tide) is indicative of low migration rates. Spittlebugs usually move by jumping and flight distances are considered to be short. The saline water surrounding the islands suggests that survival time of spittlebugs drifting on the surface will be low. Passive migration in strong winds or on rafts may be more frequent.

Although all these observations are indirect or circumstantial and studies of population dynamics are required, they suggest that the populations on the smallest islands are transient and that together they form a metapopulation. The population on each island is probably subject to fluctuations in size and extinction-recolonization events at a rate dependent in part on island size, height and successional state of the vegetation. Such events when triggered by catastrophic storms or droughts may tend to occur synchronously in particular parts of the archipelago, or they may occur in a largely independent and more continuous manner when due to factors specific to particular populations (cf. Harrison et al., 1988). Extinctions and extreme bottlenecks have probably not occurred in the history of the very large populations on each of the large islands; their populations representing a stable migrant-pool, or a series of such pools, with respect to the small islands. The subpopulations on each of the large islands are also themselves likely to exhibit the shifting mosaic type of dynamics. The isolated archipelago can, therefore, be considered to be a discrete metapopulation, within which there exist subpopulations varying in their degree of transience.

Unfortunately, there are no data describing how short-lived the different subpopulations are. The comparison of the patterns of diversity with the results of the simulations suggest that the effective number of founders or of individuals at population crashes on the smallest islands is of the order of a few tens of insects and that the genetic drift this would cause could account for the observed variance among the small island populations and the lack of overall loss of heterozygosity. Experimental perturbations of extant populations or experimental colonizations would provide further insights about the roles of population structure and dynamics, and of selection and genetic drift. The results to date emphasize the generally much greater sensitivity of the variance of diversity among subpopulations to the effects of genetic drift than of the overall mean diversity or the average heterozygosity. The work on the Isles of Scilly would be usefully extended by surveys of genotypes and across genetic loci and by studies of quantitative traits. The archipelago provides the potential for valuable studies of the effects of founder events, migration-colonization processes and the transience of subpopulations on genetic diversity within a metapopulation. The generation of variance among more transient subpopulations may have longer term consequences for such a metapopulation in terms of its capacity to respond adaptively to environmental perturbations.

Acknowledgements. I would like to thank Philip Hedrick for his suggestion to follow up further the difference in the sensitivity of the variance and mean statistics to sampling error which was apparent from initial analysis of the field data.

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