THE SCIENTIFIC MANAGEMENT OF TEMPERATE COMMUNITIES FOR CONSERVATION

THE 31ST SYMPOSIUM
OF THE BRITISH ECOLOGICAL SOCIETY
SOUTHAMPTON 1989

EDITED BY

I. F. SPELLERBERG
Department of Biology
University of Southampton

F. B. GOLDSMITH
Ecology and Conservation Unit
University College London

M. G. MORRIS
Institute of Terrestrial Ecology
Wareham, Dorset

OXFORD
BLACKWELL SCIENTIFIC PUBLICATIONS
LONDON EDINBURGH BOSTON
MELBOURNE PARIS BERLIN VIENNA

3. GENETICS AND THE CONSERVATION OF INVERTEBRATES

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

INTRODUCTION

Much of the early work on the genetics of natural populations concentrated on features of the phenotype which vary in a discrete way and are easily recognized in individuals. The Mendelian genetics of such conspicuous polymorphisms could be investigated and their effects on survival and fitness in a range of environments examined in the field or the laboratory. These studies in ecological genetics, when placed in the context of the development of the theory of population genetics, led to important insights about the frequent occurrence of strong natural selection and of adaptation to local environments (Ford 1975). Survey work following the development in the late 1960s of gel electrophoresis to investigate polymorphisms in enzymes demonstrated that very high levels of genetic variation are present in most natural populations, although the significance of much of this variability for adaptive processes is unclear (Lewontin 1974). Application of the modern technology of recombinant DNA has emphasized the high diversity which occurs at the level of nucleotide sequences in the DNA coding for particular genes. However, differences in phenotype between individuals in natural populations are usually of a quantitative rather than a discontinuous kind. Continuous variation of the sort influenced by variation at many genes is central to smooth adaptive responses to environmental change whether involving morphological, physiological, behavioural or life-history traits. Much of the current interest in evolutionary processes in natural populations is concerned with studies of such quantitative traits.

The present review examines the relevance of this development of an understanding of the genetics of natural populations to problems in the management and conservation of populations of invertebrates. It was not until around the time of the earlier symposium on conservation organized by the British Ecological Society that the vital contribution that genetics had to make to conservation biology was recognized (Berry 1971). The last decade has seen a rapidly developing awareness that genetic variation

should be considered when developing management programmes for invertebrates or other organisms (Soulé & Wilcox 1980; Frankel & Soulé 1981; Schonewald-Cox *et al.* 1983; Soulé 1986, 1987). Populations should not be considered solely as assemblages of similar individuals but rather of individuals which vary in genotype and phenotype, and thus which are likely to differ in their fitness and evolutionary potential for adaptation to environmental change.

Observations on the dynamics of natural populations have shown that most are subject to variation in numbers between generations; extreme fluctuations have been monitored in many studies. Population geneticists have analysed the ways in which changes in numbers may influence genetic variation within populations. This led to the realization that a random sampling process, known as genetic drift, is likely to lead to loss of genetic variation when populations become small and that this may decrease their subsequent ability to respond adaptively to environmental change. This review will concentrate on the effects of genetic drift to examine the problem of how much emphasis need be placed in a management programme on maintaining substantial population sizes to minimize loss of genetic variation. Attention will also be given to particular features applying to systems of interacting local populations or metapopulations. Cited population studies mostly concern species of terrestrial invertebrates, especially insects.

Many of the issues discussed in this review are also relevant to policy development in programmes involving captive breeding and introduction or reintroduction of invertebrates, although these will not be covered specifically here (see Bartlett 1985; Hedrick 1989a). There are, for example, suggestions that the success of insect introductions decreases as a function of time spent in captivity (e.g. Myers & Sabath 1981). Invertebrates in general will be comparatively sensitive to such problems because of their short generation time. Problems associated with artificial selection, inbreeding, small numbers and high variance in offspring number commonly occur in captive breeding. Artificial selection associated with the inevitable difference between captive and field environments is the only problem which is largely irrelevant to the management of natural populations.

CONSPICUOUS POLYMORPHISM AND LOCAL ADAPTATION

Genetic polymorphism is the occurrence in the same population of two or more alleles at one gene locus, each with appreciable frequency (often arbitrarily set at $>0{\cdot}01$ or $>0{\cdot}05$, see Ford 1975 and Cavalli-Sforza &

Bodmer 1971). Polymorphisms in which distinct forms or phenotypes of the colour pattern or external morphology occur have been extensively studied in species of invertebrates, especially among the Lepidoptera and Mollusca (see Ford 1975). Many such colour polymorphisms, including melanism in moths and some other arthropods, are determined by fully dominant or recessive alleles at single 'major' genes. Dominance may, however, be incomplete (see Fig. 3.4) and other polymorphisms depend on allelic variation at more than one locus sometimes with epistatic interactions between the genes at different loci (Fig. 3.1). Many instances of spatial or temporal variation in the frequency of alleles controlling colour polymorphism have been documented (Endler 1986). Sometimes allele frequencies can change sharply over remarkably short distances (e.g. Wolda 1969) or over short periods of time (see Figs 3.2 and 3.4).

Although it has been argued justifiably that the nature and intensity of natural selection and other processes which influence the evolution of colour polymorphisms are not representative of those associated with other patterns of genetic variation (Lewontin 1974), their study has led to comparatively well-understood examples of the evolution of adaptations to local, specialized environments by natural selection (see e.g. Endler 1986; Brakefield 1987). The rapid spread of melanism through many British populations of the peppered moth *Biston betularia* in response to the effects of air pollution has been particularly well-documented; the dominant *carbonaria* allele controlling the black phenotype first being recorded in Manchester in 1848 (Lees 1981). Air pollution is toxic to epiphytic lichens and darkens the tree bark on which the moths rest. The relative conspicuousness to bird predators of the pale and dark moths is, therefore, changed so that the dark melanics are favoured in industrial environments. Some such evolutionary responses have been dependent on the initial availability of appropriate genetic variation within populations. The absence of such variability, either in the form of gene mutations or rare alleles, may account for the lack of melanism as an adaptation to industrial environments in certain other species of moths in northern Europe (Kettlewell 1973).

Some urban populations of the peppered moth and of other insects such as the two-spot ladybird *Adalia bipunctata* are now experiencing rapid declines in melanic frequency apparently in response to decreases in air pollution (Fig. 3.2). The associated selective disadvantages to melanics have been estimated as about 10%, illustrating how environmental change can result in intense natural selection and rapid evolutionary responses (Cook, Mani & Varley 1986; Brakefield & Lees 1987). The short generation time of many invertebrates will tend to lead to more opportunity to

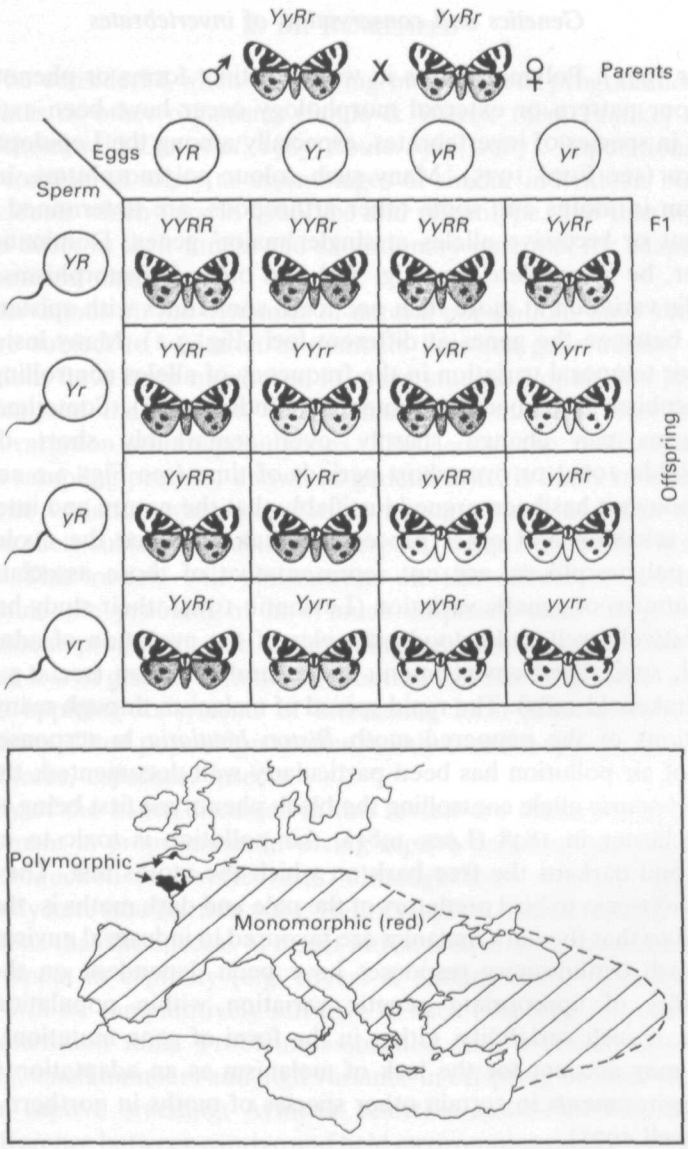

FIG. 3.1. Genetics of a conspicuous polymorphism involving an epistatic interaction between unlinked genes (from Liebert & Brakefield 1990). Colour variation of the hindwings of the jersey tiger moth *Callimorpha quadripunctaria* is illustrated: red moths, dark shading; orange moths, light shading; yellow moths, unshaded wings. This variation is controlled by two alleles with complete dominance at each of two loci, *R* and *Y*. The sixteen genotypes expected in the offspring of a cross of double heterozygotes are shown giving an expected segregation of 9 red : 3 orange : 4 yellow. Epistasis occurs since the phenotype of moths with particular genotypes at the *R* locus is dependent on the genotype at the *Y* locus. Thus, moths of the *yy* genotype are yellow irrespective of their genotype at the *R* locus. The map shows that polymorphic populations of this moth only occur in the extreme north-west of the species' range (see Brakefield & Liebert 1985).

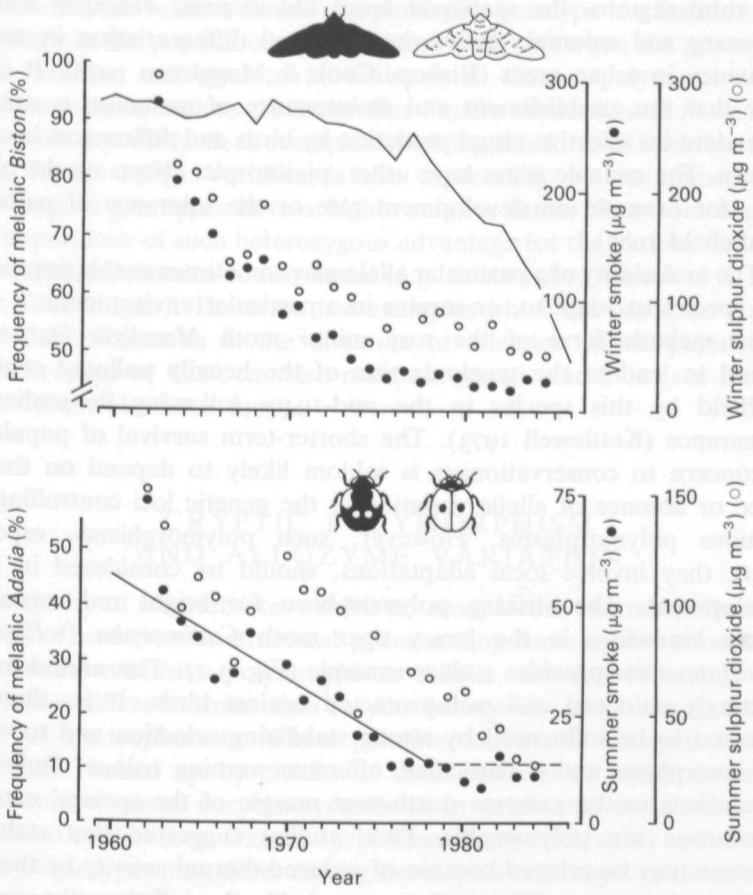

FIG. 3.2. Examples of adaptive responses to environmental change involving genetic polymorphisms. Solid lines show recent declines in the frequency of black or melanic forms of the peppered moth *Biston betularia* near Liverpool and of the two-spot ladybird beetle *Adalia bipunctata* in Birmingham. The declines are associated with falls in air pollution as shown by records from nearby monitoring stations. Changes in crypsis are involved in the case of the bark-resting moth while the ladybirds are probably influenced by changes in the screening effect of smoke on insolation (after Brakefield 1987).

'track' rapid changes in the environment with adaptive responses. Melanic polymorphisms also illustrate how the spatial scale of environmental change can interact with rates of migration and population structure to influence the pattern of adaptation. While the peppered moth, which is highly vagile and has comparatively uniform population densities, shows very smooth transitions or clines in melanic frequency between industrial

and rural regions, the scalloped hazel *Odontoptera bidentata* which is sedentary and colonial, shows marked local differentiation in melanic frequency in urban areas (Bishop, Cook & Muggleton 1978). It is also clear that the establishment and maintenance of melanism is not only dependent on selective visual predation by birds and differences in colour pattern. The melanic genes have other, pleiotropic, effects on the phenotype, for example on development rate or the tolerance of pathogens (Brakefield 1987).

The availability of a particular allele may sometimes enable populations of a species to adapt to, or survive in a particular environment; a newly arisen melanic form of the rosy minor moth *Mesoligia literosa* appeared to lead to the recolonization of the heavily polluted centre of Sheffield by this species in the mid-1940s following its earlier disappearance (Kettlewell 1973). The shorter-term survival of populations of concern to conservationists is seldom likely to depend on the presence or absence of allelic variation at the genetic loci controlling conspicuous polymorphisms. However, such polymorphisms, especially where they involve local adaptations, should be considered in policy development. The striking polymorphism for bright red, orange or yellow hindwings in the jersey tiger moth *Callimorpha (=Euplagia) quadripunctaria* provides a clear example (Fig. 3.1). This arctiid moth is warningly coloured and well-protected against birds. It is, therefore, expected to be influenced by strong stabilizing selection and to exhibit monomorphism and a particular, effective warning colour. Only those populations in the extreme north-west margin of the species' extensive distribution are polymorphic. Field studies suggested that stabilizing selection may be relaxed because of reduced diurnal activity by the moth in this cooler region. Climatic factors probably also influence the variation via pleiotropic effects of the genes which are important in this specialized, marginal environment (Brakefield & Liebert 1985). Similar arguments concerning populations of particular evolutionary interest can be applied to zones of hybridization (Hewitt 1988) and groups of populations with the taxonomic status of subspecies or races.

Three major forms of natural selection are commonly recognized: directional selection favours an extreme expression of a trait; stabilizing selection favours an intermediate expression and disruptive selection simultaneously favours more than one phenotype. Stabilizing or optimizing selection tends to reduce genetic variance. In a population at equilibrium there may be a balance between such selection and gene mutation (e.g. Lande & Barrowclough 1987). Selection which is frequency-dependent is probably of particular significance in maintaining genetic variation in natural populations (Clarke 1979; Endler 1986). Frequency dependence

occurs when the relative fitness of a particular genotype is a function of its frequency in the population. If the fitness is highest when the genotype is rare, variation will tend to be maintained. Colour polymorphisms in Batesian mimics, such as the butterflies *Papilio dardanus* and *P. memnon* L. provide especially clear examples involving this form of selection (Ford 1975; Turner 1984). Variation is also expected to be maintained when heterozygote genotypes have a higher relative fitness than homozygotes. The importance of such heterozygous advantage for the various classes of polymorphism remains controversial (e.g. Soulé 1980; Allendorf & Leary 1986; Endler 1986). There are few examples which are based on unequivocal data. Variation in the direction of selection within populations, either in space or time, can also maintain genetic variation (see Hedrick 1986, 1989b; Hoekstra 1975).

CRYPTIC POLYMORPHISM AND ALLOZYME VARIATION

The majority of invertebrates exhibit no conspicuous polymorphisms, but surveys of variation at structural genes coding for enzymes consistently demonstrate extensive polymorphism. Allelic variation of such a gene determines different forms of an enzyme (allozymes) which can be assayed using gel electrophoresis. Where possible, surveys of allozyme variants should be backed up by checks of their patterns of inheritance. The expression of some enzyme systems in invertebrates is known to be influenced by diet (e.g. Oxford 1975; Klarenburg *et al.* 1988) and in other cases, phenotypes may differ among developmental stages or tissue types (Colgan 1989). The application of more recently developed recombinant DNA technology to analyse both nuclear and mitochondrial DNA sequences directly has emphasized the variation present between individuals in structural genes, as well as in non-coding regions of the DNA (see Ayala 1984; Quinn & White 1987). Genetic variation at the level of the DNA is evidently substantially more extensive than that detected by electrophoresis (e.g. for the alcohol dehydrogenase locus [Adh]; see Krietman & Aguadé 1986). The general significance of this variation for processes of adaptation is unclear (Lewontin 1974; Dover 1986; Hedrick *et al.* 1986; Eanes 1987).

Studies of a small number of enzyme polymorphisms have provided evidence that allele frequencies can be influenced by natural selection and that populations in particular ecological environments can exhibit predictably high frequencies of particular alleles controlling allozymes with specific biochemical properties. Two well-worked examples are Adh in *Drosophila* (Van Delden 1982) and phosphoglucoisomerase (PGI) in *Colias*

butterflies (Watt 1977; Watt, Cassin & Swan 1983; Watt, Carter & Blower 1985). The Adh gene has a central role in ethanol detoxification, and genotypes which increase flux through this pathway are more common in wineries and survive better on media containing alcohol. The PGI system provides compelling evidence that heterozygous genotypes are favoured in some populations, thus tending to maintain the genetic variation. The allozymes of PGI differ in their thermal stability and in their effectiveness as catalysts involved in glycolysis and energy metabolism; these differences influencing mating success, survival and other components of fitness in natural populations. In contrast, many studies of variability in other enzymes have failed to provide convincing evidence of any influence on fitness (see Endler 1986). Many, perhaps most, alleles controlling allozymes probably have a negligible, or no effect on fitness under the prevailing environmental conditions; thus, they are neutral or effectively neutral.

MEASURES OF HETEROZYGOSITY AND ALLELIC DIVERSITY

The extent of variation at enzyme loci which is detectable through electrophoretic mobility has been surveyed for various classes of animals by Powell (1975), Selander (1976), Nevo (1978) and Nevo, Beiles & Ben-Shlomo (1984). The proportion of loci which are polymorphic (P) in invertebrates averages about 40% which is nearly twice as high as in vertebrates. Similarly, the mean heterozygosity of around 12% is about three times higher. In a population which is in Hardy–Weinberg proportions the amount of heterozygosity at a locus (H) is the probability that two randomly chosen alleles are different:

$$H = 1 - \sum \hat{p}_i^2$$

where $\hat{p}_i$ is the frequency of the ith allele. In practice, there are several ways in which this can be estimated: from observed frequencies of heterozygotes, from expected frequencies (assuming Hardy–Weinberg proportions) or from allele frequency data. The mean heterozygosity ($\bar{H}$) in a population is usually calculated for a number of loci. It is equivalent to the mean proportion of individuals which are heterozygous when averaged across all loci surveyed. Again, it can be estimated in different ways, each of which influences the amount of variance associated with the parameter. If a population is not in Hardy–Weinberg proportions because, for example, matings between relatives are common, the observed heterozygosity may not reflect closely the amount of genetic variation

or genic diversity in the population. However, in most outbreeding animal populations, genotypes at enzyme loci are near Hardy–Weinberg proportions.

An estimate of heterozygosity for a representative survey of some twenty or so enzymes in a sample is unlikely to be closely correlated with overall genomic heterozygosity (Chakraborty 1981; Hedrick *et al.* 1986). Thus, it cannot be recommended as a general indicator of genetic variation or, in a broader sense, of fitness. Heterozygosity also provides little information about allelic diversity, either with respect to the number of alleles (n) or the distribution of allele frequencies (Allendorf 1986; Fuerst & Maruyama 1986). In particular, H is highly dependent on the frequencies of the common alleles and, conversely, it is very insensitive to the presence or absence of rare alleles. Many alleles within natural populations are only represented at low or very low frequencies; allele frequency distributions tend to be U- or J-shaped (Chakraborty, Fuerst & Nei 1980). Rare alleles could provide the potential for adaptive responses to novel environments; examples are known from studies of responses of populations to man-made changes in their environment (Bishop & Cook 1981). In such cases populations having a rare allele which becomes advantageous following an environmental change are said to be preadapted. Low-frequency alleles contribute little to the immediate response of a population to selection but the magnitude of the long-term response over many generations can be determined by the initial allelic diversity present (Robertson 1960; James 1971; Mather 1982). Reliable data for allelic diversity can be difficult to obtain; n is very sensitive to sample size and it gives equal weight to all alleles regardless of their frequency.

Wright's (1931, 1943, 1951) fixation indices can be used for comparisons of genetic diversity across populations and studies of the genetic consequences of population structure (e.g. Santos, Ruiz & Fontdevila 1989). These indices were defined by Wright as the correlations in genetic variation between uniting gametes relative to the subpopulation (F_{IS}) and to the total population (F_{IT}). F_{ST} is the correlation of random gametes within subpopulations relative to the total population; it is a measure of the standardized among-population component of genetic variance. Nei (1977, 1987) reformulated F statistics as functions of observed and expected heterozygosities.

The interpretation of F statistics obtained for natural populations is rather controversial (see Nei 1986, 1987). They can undoubtedly be valuable in formulating hypotheses about the relative importance of random genetic drift, gene flow and selection in influencing spatial patterns of genetic differentiation (e.g. Allendorf 1983; Slatkin 1985, 1987). Gene

flow between populations acts as a unifying influence. Neutral alleles will tend to diverge in frequency among isolated (closed) populations due to the sampling effects of genetic drift (see p. 62). Relatively low rates of gene flow will overcome this effect. Wright (1931) showed that for neutral alleles, $F_{ST} \approx 1/(1 + 4\,Nm)$ where N is the size of the local population, subpopulation or deme, and m is the average rate of immigration in an 'island' model of population structure. In such a model, migration refers to the exchange of reproductively successful individuals among demes and the rate of migration among the equal-sized colonies is independent of the distance between them. Migration in this sense will thus result in gene flow between demes while migration in an ecological sense may not necessarily do so. Higher rates of gene flow are required to overcome the influence of differences in directional selection among populations (e.g. Allendorf 1983). Other models of gene flow include 'isolation by distance' in which populations are continuously distributed and gene flow is described by a continuous probability distribution function, and one- or two-dimensional 'stepping-stone' models where gene flow is predominantly between adjacent populations. These have differing implications for spatial differentiation (see Rockwell & Barrowclough 1987).

The effects of gene flow are illustrated by analysis of data for allelic variation for eight enzymes in twenty-one Californian populations of the butterfly *Euphydryas editha* (Table 3.1). Ecological studies suggest that for these populations *Nm* is of the order of 0·01; migration rates are very low. Seven of the eight enzyme loci show much more similarity across populations than can be accounted for by present-day patterns of gene flow. Either selection is influencing the seven polymorphisms in similar

TABLE 3.1. Values for the fixation index (F_{ST}) and estimates of *Nm* derived from data of McKechnie, Ehrlich & White (1975) describing allelic variation at each of the indicated enzyme loci in twenty-one Californian populations of *Euphydryas editha* (from Slatkin 1987).

Enzyme locus	F_{ST}	*Nm*	
pgm	0·028	8·7	
pgi	0·052	4·6	
got	0·017	14·5	
ak	0·062	3·8	mean = 7·8
bdh	0·034	7·1	
α-gpdh	0·027	9·0	
to	0·035	6·9	
hk	0·291	0·6	

ways across populations or the patterns are relics of substantial gene flow and more continuous habitats in the past. The difference in the *F*-statistic for the eighth locus (*hk*) indicates that either it, or a closely linked locus, is strongly influenced by selection (Slatkin 1987). Gene flow in many other invertebrates, such as many marine species with planktonic larvae or arthropods with wind-dispersed life stages, will be much more extensive for present-day populations.

POLYGENIC VARIATION AND QUANTITATIVE CHARACTERS

The majority of adaptive responses to environmental changes involve phenotypic traits which vary in a continuous manner (Falconer 1989). The traits may concern morphology, physiology, life history, behaviour or any other feature of the phenotype. The phenotypic variation (V_P) in any continuous or quantitative trait can be partitioned into environmental (V_E) and genetical (V_G) components or effects on its development:

$$V_P = V_E + V_G$$

(there is also a covariance term describing the distribution of genotypes across environments). Quantitative characters are influenced by many genes (polygenes) each of small effect on the phenotype. The effective number of loci influencing a typical character has been estimated to range from about 5 or 10 up to 20 (Lande 1981).

The genetic variance can be further partitioned into statistically additive (V_A) and non-additive (V_{NA}) effects of alleles within and among loci. A simple case of additivity would involve two genes which when acting alone each produce a phenotype of 1 unit, while when acting in concert produce one of 2 units. Non-additivity arises either from dominance of alleles at the same locus (V_D) or from epistatic interactions between alleles at different loci (V_I, see Fig. 3.1):

$$V_P = V_E + V_A + V_D + V_I.$$

Genetical analyses of quantitative traits usually concentrate on attempting to partition the phenotypic variance (Lawrence 1984; Falconer 1989). The components can be analysed only by indirect, statistical means. They can all be estimated from phenotypic correlations between relatives. The contribution of the additive genetic variance is of particular importance since it indicates how rapidly the quantitative character would be expected to respond to selection. The heritability (h^2) of a character describes the contribution to the phenotypic variance of the additive genetic

effects relative to environmental influences during development:

$$h^2 = V_A/V_P.$$

Heritability is frequently estimated from the resemblance between families of offspring and their parents. Figure 3.3 illustrates this relationship and the responses to directional selection expected in populations exhibiting differences in heritability. A low heritability and small additive genetic variance is expected to lead to a slow shift in the mean value of a character in a population in response to directional selection such as might be associated with an environmental perturbation. If variation in a character is entirely dependent on environmental effects there is no evolutionary potential. A high heritability is likely to result in a rapid response to directional selection.

When considering the consequences of an estimate of heritability derived in the laboratory for a managed population it is important to bear in mind that, strictly speaking, such an estimate applies only to the particular stock and the particular laboratory environment used in the experiment. Estimates are dependent on allele frequencies within the stock, and laboratory environments are usually less variable than in the field and will, therefore, tend to lead to overestimates of natural heritabilities (see Boag & van Noordwijk (1987) for further discussion of the limitations). Typical characters with a moderate heritability yield estimates of h^2 of 0·3–0·6 (see examples in Fig. 3.10).

There has been an expanding interest in the genetical relationships, measured as genetic covariances or correlations, between quantitative characters. Such covariances, which are based on some genes exhibiting effects on more than one character (pleiotropy), may constrain evolutionary responses (Via & Lande 1985); a negative genetic correlation would, for example, tend to slow a positive response to directional selection influencing the two characters in a parallel way. A possible example of the involvement of genetic covariances are switches in host-plant preferences by phytophagous insects where larval performance on a host and oviposition preference covary (e.g. Via 1984, 1986; Singer, Ng & Thomas 1988).

Studies of quantitative variation in wild populations of insects (e.g. Lande & Arnold 1983; Koenig & Albano 1987) suggest that natural selection may often focus on a small subset of characters during sporadic intervals of extreme environmental conditions. The genetic variance–covariance matrices underlying phenotypic variation in such subsets of characters will be critical in determining the evolutionary response to novel environments. The longer-term fitness of a natural or managed population or, in simple terms, its ability to adapt to environmental

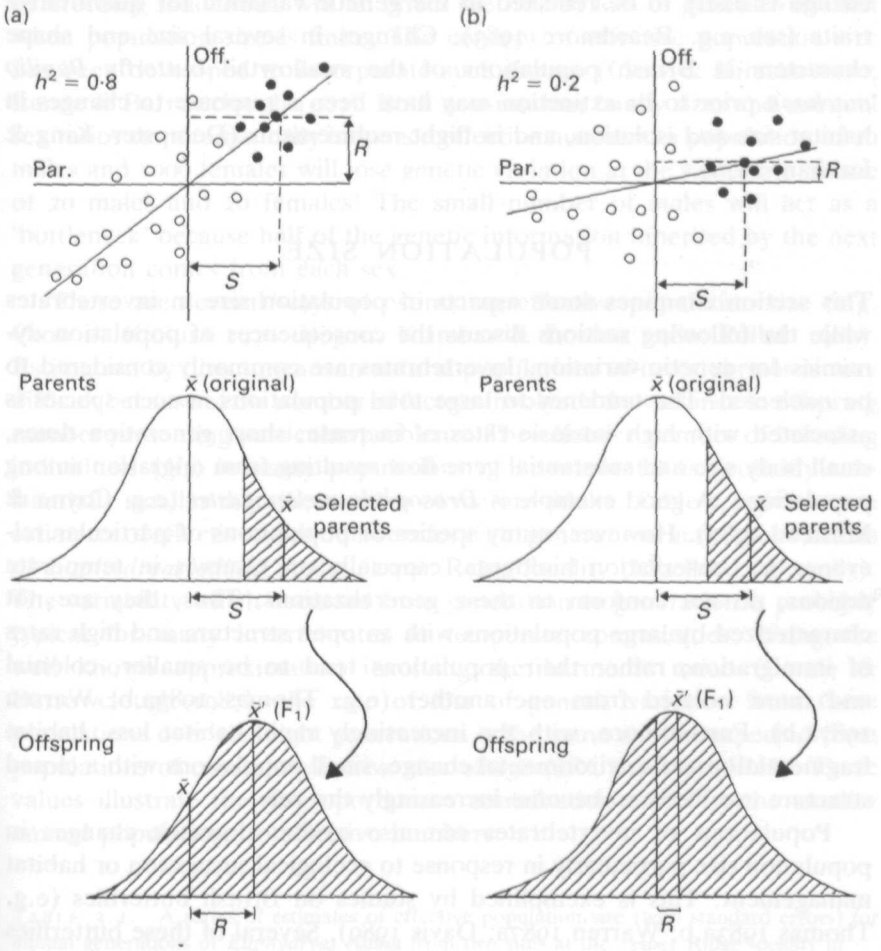

FIG. 3.3. Relationships between heritability, parent–offspring regression and the response to selection for a hypothetical trait with either a high (a), or a low (b) contribution of additive genetic variance to phenotypic variation. The upper diagrams show the resemblance between offspring and their parents for a heritability of 0·8 and one of 0·2 (as given by the slopes of the fitted regression lines). The middle part shows frequency distributions of the trait in hypothetical parental populations with shading indicating the occurrence of directional selection when only the largest or more extreme 25% of individuals in these populations are successful in reproducing themselves (S is the selection differential). The lower distributions illustrate the predicted response (R) in the mean value for the trait in populations of their offspring given the high or the low heritability (redrawn from Boag & Noordwijk 1987).

change is likely to be reflected in the genetic variation for quantitative traits (see e.g. Beardmore 1983). Changes in several size and shape characters in British populations of the swallowtail butterfly *Papilio machaon* prior to its extinction may have been a response to changes in habitat size and isolation, and in flight requirements (Dempster, King & Lakhani 1976).

POPULATION SIZE

This section examines some aspects of population size in invertebrates while the following sections discuss the consequences of population dynamics for genetic variation. Invertebrates are commonly considered to be *r*-selected. The tendency to large total populations in such species is associated with high intrinsic rates of increase, short generation times, small body size and substantial gene flow resulting from migration among populations. A good example is *Drosophila melanogaster* (e.g. Coyne & Milstead 1987). However, many species or populations of particular relevance to conservation biologists, especially on reserves in temperate regions, do not conform to these generalizations. Thus, they are not characterized by large populations with an open structure and high rates of immigration; rather their populations tend to be smaller, colonial and more isolated from one another (e.g. Thomas 1983a,b; Warren 1987a,b). Furthermore, with the increasingly rapid habitat loss, habitat fragmentation and environmental change, small populations with a closed structure are likely to become increasingly the rule.

Populations of invertebrates can also exhibit dramatic changes in population size particularly in response to ecological succession or habitat management. This is exemplified by studies on British butterflies (e.g. Thomas 1983a,b; Warren 1987a; Davis 1989). Several of these butterflies occur in ecologically marginal regions which are likely to be especially prone to the effects of small and fluctuating population sizes and the subdivision of populations (see Brussard 1984). They are also likely to exhibit local adaptations to specialized physical or ecological environments (see Fig. 3.1 and p. 50).

The absolute size of a population of reproductively mature animals may not be closely related to the proportion of genetic variation transmitted to the next generation. Clearly, if only a small proportion of the individuals breed and contribute to the next generation, the effective size of the population from a genetical perspective will be correspondingly much reduced. Such factors as the sex ratio, non-random variability in the number of offspring per individual and temporal fluctuations in the number

of breeding individuals will all affect the rate of loss of genetic variation when population size is finite. The concept of effective population size has been developed to incorporate such factors (Crow & Kimura 1970; Lande & Barrowclough 1987). Both non-random family sizes and unequal sex ratios can dramatically influence effective numbers; a population of 10 males and 1000 females will lose genetic variation at the same rate as one of 20 males and 20 females! The small number of males will act as a 'bottleneck' because half of the genetic information inherited by the next generation comes from each sex.

There are several ways of estimating effective population size (e.g. Crow & Kimura 1970; Begon, Krimbas & Loukas 1980; Pollak 1983). Estimation by direct means in natural populations of invertebrates is very difficult because of the number of factors involved; the variance in offspring number presenting particular problems. The effective number of breeding individuals (N_e) in many populations of invertebrates is probably substantially smaller than the number of mature adults. Table 3.2 gives some estimates of effective adult numbers for eight generations in two populations of *Euphydryas editha* at the Jaspar Ridge locality (Mueller *et al.* 1985). The variability which occurred from generation to generation is probably typical for many invertebrates in temperate communities. Using the well known approximation involving the harmonic mean (Lande & Barrowclough 1987), the rate of loss of genetic variation from these populations over the eight generations is the same as that expected from populations of constant effective size of 138 (JRC) and 50 (JRH). These values illustrate the disproportionate contribution made by the smaller annual populations to effective numbers.

TABLE 3.2. A series of estimates of effective population size (with standard errors) for annual generations of *Euphydryas editha* from two sites at the Jasper Ridge locality in California (from Mueller *et al.* 1985).

Year	Site C		Site H	
	N_e	S.E.	N_e	S.E.
1973	762	366	144	18
1974	164	24	28	3
1975	856	135	93	7
1976	4022	786	974	149
1977	374	6	179	18
1978	28	4	17	2
1979	182	21	33	3
1980	195	32	90	13

The long series of estimates of adult numbers in an Oxford colony of the scarlet tiger moth *Callimorpha (=Panaxia) dominula* also show how variable population size can be. In this example, a progressive decrease in the frequency of an allele controlling features of wing pattern was not correlated with the changes in population size (Fig. 3.4). Although effective population sizes may have been very much lower than those estimated, there appears little doubt that this allele suffered a selective disadvantage but the mechanism of selection remains unknown.

To summarize this section: populations of many invertebrates may be subject to intermittent population crashes and, therefore, pass through 'bottlenecks' in numbers. A similar phenomenon will occur when a population is established from a small number of founder individuals. In each of these situations, the effective population size is likely to be (much) smaller than the actual number of individuals present. Such a discrepancy will accentuate the genetic effects of any reduction in population size. Estimates of effective numbers in small populations of invertebrates of concern to conservationists are needed.

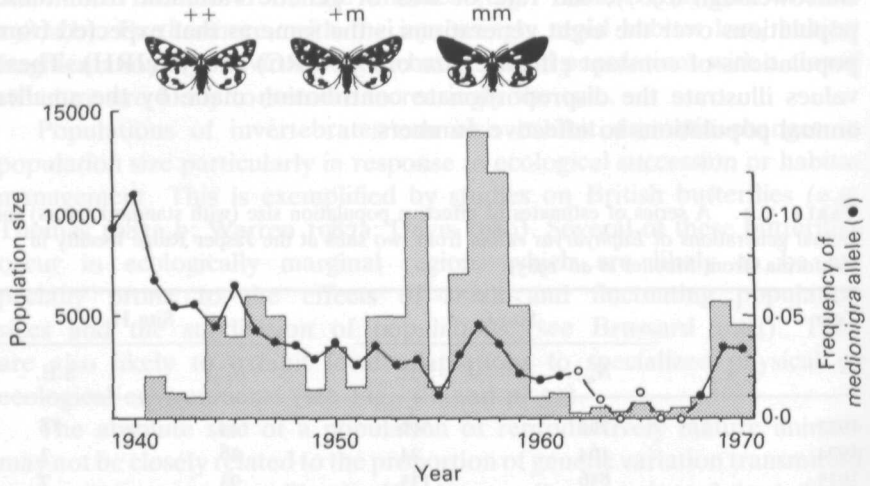

FIG. 3.4. Relationship between population size and the frequency of the *medionigra* allele (*m*) determining the illustrated variation in wing pattern of the scarlet tiger moth *Callimorpha dominula* at Cothill Fen. The wild type (+) and *medionigra* alleles exhibit incomplete dominance. Estimates of allele frequency are shown by circles with open symbols indicating estimates based on fewer than 100 moths (data from Ford 1975; after Parkin 1979).

POPULATION BOTTLENECKS: LOSS OF POLYMORPHISM AND HETEROZYGOSITY

A well-developed body of theory describes the expected loss of heterozygosity for neutral alleles due to random genetic drift when a (closed) population passes through a bottleneck of small effective size. Genetic drift refers to chance changes in allele frequencies as a result of random sampling among gametes from generation to generation (Hartl 1980). It has a greater effect upon small populations because small samples are frequently not representative. The expected proportion of the original heterozygosity remaining after a bottleneck is:

$$1 - \frac{1}{2N_e}.$$

Table 3.3 shows that even very small populations are actually expected to retain a substantial proportion of heterozygosity after a bottleneck lasting for only one generation. However, the table also shows the more profound effects of more prolonged periods of small size (see Nei, Maruyama & Chakraborty 1975; Janson 1987). The consequences of a crash in numbers in a managed population are, therefore, expected to be dependent not only on the size of the original bottleneck but also on the rate of recovery in effective numbers. The following expression describes the loss of heterozygosity expected over a sequence of t generations:

$$\bar{H}_t = H_0 \exp^{-t/2N}.$$

The heterozygosity in the two populations of *E. editha* at Jasper Ridge is then expected to have declined by 3% (JRC) and 8% (JRH) from 1973 to 1980 (Table 3.2).

TABLE 3.3. Percentage of the original heterozygosity for neutral alleles expected to remain after bottlenecks of various sizes lasting for the indicated number of generations (after Allendorf 1986).

Bottleneck size (N)	Duration of bottleneck (generations)		
	1	10	100
2	75	6	0
4	85	26	0
10	95	60	1
25	98	82	13
50	99	90	37
100	100	95	61

Figure 3.5a shows examples of the expected rate of loss of allelic diversity at a locus after single-generation bottlenecks. Unfortunately as Allendorf (1986) has emphasized, the assumption of equal frequency of the alleles is unrealistic. Figure 3.5b shows how rare alleles are especially susceptible to loss during a bottleneck. To take a simple and extreme case: a bottleneck of a single pair will constitute only four copies of a single gene, so that the probability of losing an allele originally at a frequency of 0·01 is $(0{\cdot}99)^4 \approx 0{\cdot}96$. Similarly, about 60% of such alleles will be lost after a single-generation bottleneck of twenty-five individuals.

The three main effects of genetic drift associated with small populations are: heterozygosity is expected to decline, rare alleles are expected to be lost and variance among populations is expected to increase. The effect of an episode of genetic drift depends on: (i) heterozygosity and allelic diversity prior to the sampling event; (ii) the effective population size at the sampling event; (iii) the number of generations over which the bottleneck occurs; (iv) the rate of increase in effective numbers thereafter; (v) the distribution of fitness values over alleles and loci (selection); and (vi) the amount of gene flow from other demographic units.

Another form of sampling error happens when mating tends to occur between relatives. This is also more likely to be associated with small populations and has similar consequences to genetic drift. Such inbreeding increases the proportion of homozygous gene loci. It can, therefore, be

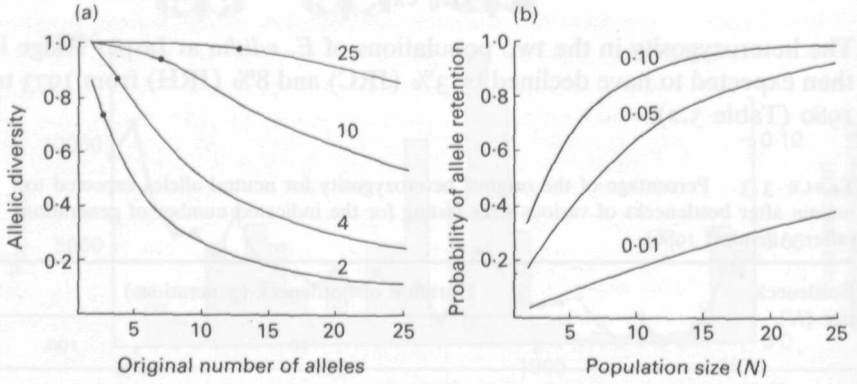

FIG. 3.5. The effect of bottlenecks in population size on allelic diversity. (a) Original number of alleles plotted against proportion of allelic diversity remaining after a bottleneck of a single generation of 2, 4, 10 or 25 individuals. All alleles are assumed to be equally frequent. Solid circles indicate the proportion of heterozygosity ($\bar{H}$) expected to be retained. (b) The probability of retaining a rare allele (at frequency 0·01, 0·05, or 0·1) after a single-generation bottleneck of size N (redrawn from Allendorf 1986).

associated with: (i) an increasing expression of detrimental recessive alleles; (ii) decreasing frequencies of individuals exhibiting heterozygous advantage; and (iii) decreasing variability among offspring. These effects are all likely to reduce the potential for adaptation, although I am not aware of any studies of the consequences of inbreeding in natural populations of invertebrates.

LABORATORY AND FIELD STUDIES OF POLYMORPHISM

The three main effects of genetic drift at bottlenecks have been documented many times in laboratory populations, especially of *Drosophila* and *Tribolium* (e.g. Buri 1956; Dobzhansky & Pavlovsky 1957; Rich, Bell & Wilson 1979; Wool 1987).

There are also numerous data sets showing differences in allozyme variation among natural populations of invertebrates which have been interpreted as evidence for genetic drift associated with bottlenecks or small founding populations (e.g. Janson 1987; Black *et al.* 1988; work cited in Wool 1987). Data for colour polymorphisms in a spider and a snail show how historical disturbance of habitats and the populations they support can produce genetic differentiation among populations through genetic drift (Goodhart 1973; Cameron & Dillon 1984; Oxford & Shaw 1986; Oxford 1989). Here I will illustrate some of the effects of genetic drift using data describing the frequency of colour pattern phenotypes, controlled by a series of alleles at a major gene locus, in populations of the rather sedentary homopteran *Philaenus spumarius* in the Isles of Scilly (Brakefield 1989, 1990). This isolated archipelago is located off south-west England and was formed essentially from a single granitic land mass some 1500 years or generations ago. Large samples of the spittlebug were obtained from twenty-six islands varying in size from 0·2 to 622 ha.

Six alleles are present in the Isles of Scilly. Two common alleles with frequencies of 0·88 and 0·10 determine three non-melanic phenotypes (Fig. 3.6). A series of melanic forms which are each at a low or very low frequency is controlled by other alleles. One of these alleles was detected only on one small island where it was, however, at a frequency of about 0·08. It may have originated *in situ* as some form of mutation; if the population was then small, the allele may have been at an appreciable frequency throughout its history.

The smaller islands support populations which are more variable in heterozygosity at this locus than the larger islands (Fig. 3.6). This pattern is not an artefact of variation in sample size and appears to be the result

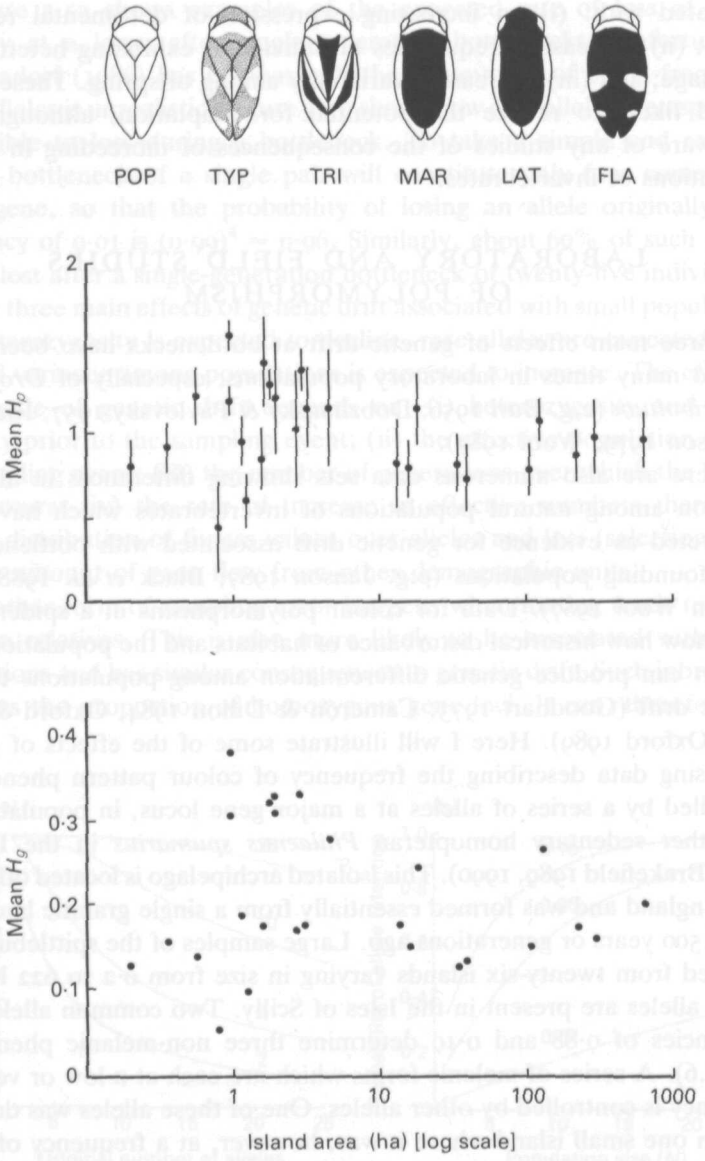

FIG. 3.6. (a) Phenotypic diversity (H_P) and (b) genic diversity (heterozygosity, H_g) in samples of female spittlebugs, *Philaenus spumarius*, from islands of varying size in the Isles of Scilly archipelago. The most frequent phenotypes are illustrated (with abbreviated names) with three non-melanics to the left and three melanics to the right. The phenotypic variation is controlled by a series of alleles at a single locus. Populations on smaller islands show greater variability in diversity indices apparently due to the effects of genetic drift. Bars in (a) indicate 95% confidence limits (from Brakefield 1989).

of genetic drift associated with winter storms inundating the small, low-lying islands to produce intermittent bottlenecks or founder events associated with extinction–recolonization cycles. Three of the ten smallest islands which were sampled showed no melanics in large samples and, therefore, appeared to represent cases of loss of rare alleles through genetic drift. This rate of fixation of alleles is consistent with bottlenecks or founding populations equivalent to effective numbers of the order of thirty insects. Simulations show that such bottlenecks would produce substantially increased variance among island populations with little change in the mean value of heterozygosity across islands (Fig. 3.7). This is similar to the pattern evident in the natural populations (Fig. 3.6). The loss of rare alleles in, and the variance in genetic diversity among subpopulations are much more sensitive to genetic drift than is the heterozygosity averaged across subpopulations.

METAPOPULATION STRUCTURE

The populations of the smaller islands in the Isles of Scilly appear to conform to a 'shifting mosaic' type of population dynamics. Levins (1970) used the term metapopulation to describe such a system of interacting local populations in which individual subunits may become extinct and subsequently be recolonized by immigration from other subpopulations which have remained viable. Not all the smaller islands in the Isles of Scilly had been colonized at the time of sampling. Total populations on the largest islands are extremely large and very unlikely to experience bottlenecks. This proposed structure is closely similar to that described in detail for the checkerspot butterfly *Euphydryas editha* in part of California (Harrison, Murphy & Ehrlich 1988) and likely to be paralleled in many other invertebrates including the butterflies *Lysandra bellargus*, *Thymelicus acteon* and *Mellicta athalia* in southern England (Thomas 1983a,b; Warren 1987b). The distribution of local populations of the checkerspot butterfly was predictable from a series of habitat variables and distance from a source of colonists. High rates of turnover of local populations may be characteristic of small patches of low quality. Many local populations of invertebrates, including these butterflies, are likely to have become successfully established from a small number of founders; this is known to have been the case for some natural colonizations or reintroductions of butterflies to individual sites in Britain (Oates & Warren 1989).

The extent of genetic differentiation within a metapopulation depends on turnover rates, the patterns of movement between habitat patches and

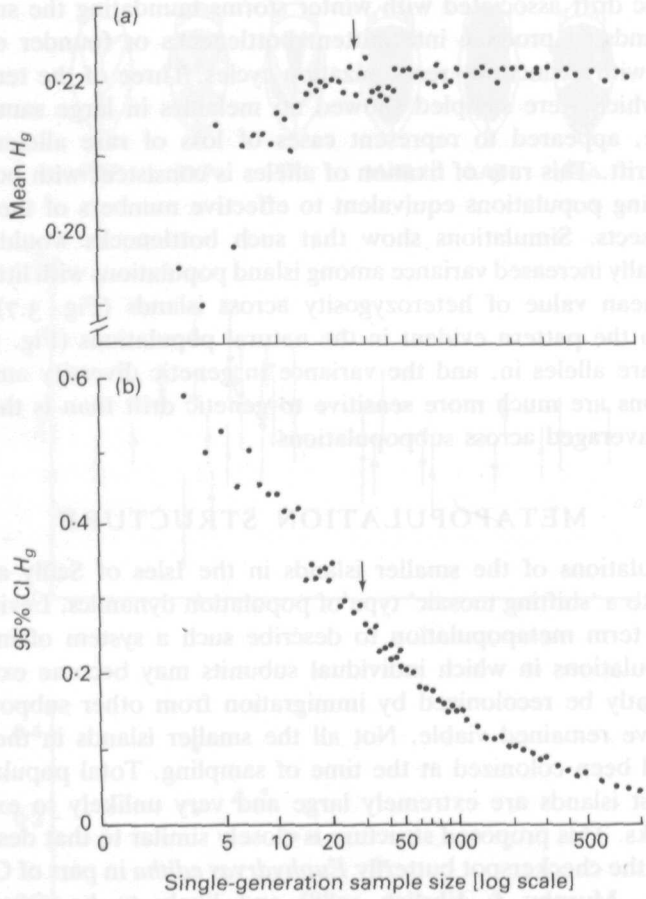

FIG. 3.7. Results from simulations involving applying single-generation sampling effects (bottlenecks) to a hypothetical 'total' Isles of Scilly population of the colour-polymorphic spittlebug *Philaenus spumarius* (see Fig. 3.6): (a) mean index of genic diversity (heterozygosity, H_g), and (b) 95% confidence interval of H_g. Arrows indicate the magnitude of sampling effect yielding a rate of loss of the rare melanic alleles similar to that observed among the smallest islands (from Brakefield 1989).

on the relative magnitudes of the number of colonists and the number of migrants moving between extant populations (Wade & McCauley 1988). The survival of a metapopulation and its particular genetic structure will thus depend not only on the persistence and number of extant populations and the availability of empty suitable habitat patches, but also on the spatial arrangement of all patches and the suitability of intervening habitat for migratory movement (Quinn & Hastings 1987; Murphy & Weiss 1988;

Hanski 1989). If the establishment of nature reserves or the management of habitats within them results in isolation of only a (small) proportion of the subpopulations which were formerly part of a larger metapopulation this may decrease the chance of persistence of the whole unit (see Hanski 1989). Movements between extant populations may reduce any deleterious effects of genetic drift or mating between relatives in small populations such as those which would otherwise be likely in some of the local populations of *E. editha* at Jasper Ridge (see Table 3.2; Mueller *et al.* 1985).

BOTTLENECKS AND POLYGENIC VARIATION

Genetic drift is expected to result in loss of additive genetic variance in a similar way to allelic variation at individual loci (Franklin 1980; Lande & Barrowclough 1987). Thus, the expected loss in V_A in a single-generation bottleneck is $1/2N_e$ (Lande 1980). Franklin (1980) reported that laboratory experiments, although far less extensive than for polymorphic traits, indicated a decline in heritability of morphological traits following extreme bottlenecks.

The restoration of variation in neutral alleles at individual polymorphic genes will only occur very slowly (on the scale of the reciprocal of the mutation rate = 10^5–10^6 generations). Although additive genetic variance for a quantitative trait will recover more rapidly, the time-scale of a few hundred or a few thousand years is still unlikely to be very relevant to conservation programmes. Franklin (1980) proposes from considerations of the theoretical relationships between genetic drift, mutation and population dynamics, that to maintain most of the additive genetic variance, the minimum effective size of a population should be 50 in the short-term or 500 in the long-term. The derivation of these guide numbers and the problem of what is, or should be, implied from 'short-term' or 'long-term' is discussed further by Soulé *et al.* (1986), Lande & Barrowclough (1987) and Pimm, Jones & Diamond (1988). Problems of time horizons are frequently discussed on a scale of years which takes no account of generation time. The short generation time of most invertebrates will clearly present more opportunity for loss of genetic variation than in organisms with longer generation times.

BRYANT'S EXPERIMENTS WITH HOUSEFLIES

The historical treatment of quantitative characters in the context of conservation has concentrated on additive genetic variance. Some important

bottleneck experiments performed by E. Bryant using the housefly *Musca domestica* and some recent development of theory by C. Goodnight show that more attention should be paid to non-additive components of genetic variance and interactions between genes.

The basic experimental design used by Bryant, McCommas & Combs (1986) and Bryant, Meffert & McCommas (1990) is illustrated in Fig. 3.8. Variability at four polymorphic enzyme loci, in eight morphometric traits and in several variables related to fitness and viability was monitored in experimental lines established from a natural outbred population and subjected to a series of five bottlenecks of one, four or sixteen pairs of flies. Each line was allowed to 'flush' following a bottleneck up to a population size of about 1000 pairs. Controls were maintained at around this level. Allozyme heterozygosity declined roughly as expected in the bottleneck lines (Bryant, Meffert & McCommas 1990).

The first important phenomenon that this experiment illustrates is that individual selection can (rapidly) restore initial loss of fitness associated with genetic drift (or inbreeding). Figure 3.9 shows how in most experimental lines, including one experiencing single-pair bottlenecks, loss of viability was transient with recovery occurring over the course of the experiment. This appears to have been the result of individuals of relatively high fitness due to their particular genetic properties contributing more offspring in earlier generations than the majority of other individuals of reduced viability. The single-pair bottleneck line which showed a final viability comparable to the controls also showed a much reduced heterozygosity at the enzyme loci by the end of the experiment. This illustrates again that

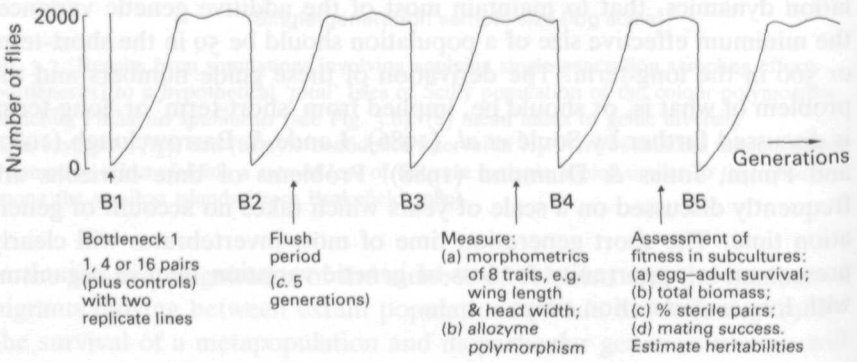

FIG. 3.8. Design of the experiments of E. Bryant to investigate the effects of a sequence of single-generation bottlenecks on genetic variation in lines of the housefly *Musca domestica* established from a single large natural population. Measurements or estimates were made following the flush period after each bottleneck.

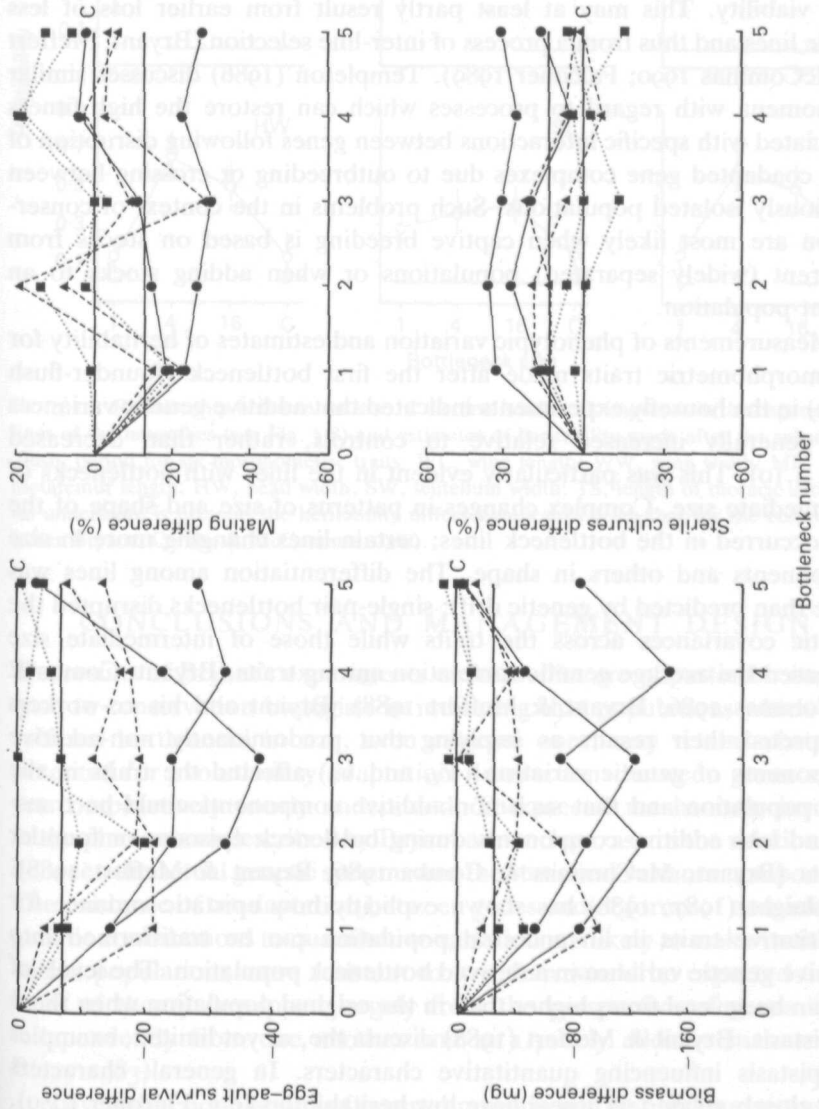

FIG. 3.9. Changes in four components of fitness in subcultures taken from the bottleneck lines of the housefly population (see Fig. 3.8). Size of bottleneck: one pair (●); four pairs (▲); sixteen pairs (■). Each component is measured relative to values for controls as represented by the indicated solid line (C). The other solid line shows a one-tailed 95% confidence interval for the difference (after Bryant, Meffert & McCommas 1990).

there may be little correspondence between electrophoretic variability and fitness. It is also well known that highly inbred (and homozygous) lines of *Drosophila* and other organisms which have been maintained over many generations can, at least in laboratory environments, exhibit high viability. This may at least partly result from earlier loss of less viable lines and thus from a process of inter-line selection (Bryant, Meffert & McCommas 1990; Falconer 1989). Templeton (1986) discusses similar phenomena with regard to processes which can restore the high fitness associated with specific interactions between genes following disruption of such coadapted gene complexes due to outbreeding or crossing between previously isolated populations. Such problems in the context of conservation are most likely when captive breeding is based on stocks from different (widely separated) populations or when adding stocks to an extant population.

Measurements of phenotypic variation and estimates of heritability for the morphometric traits made after the first bottleneck (founder-flush cycle) in the housefly experiments indicated that additive genetic variances had generally increased relative to controls, rather than decreased (Fig. 3.10). This was particularly evident in the lines with bottlenecks of intermediate size. Complex changes in patterns of size and shape of the flies occurred in the bottleneck lines; certain lines changing more in size components and others in shape. The differentiation among lines was more than predicted by genetic drift; single-pair bottlenecks disrupted the genetic covariances across the traits while those of intermediate size increased the average genetic correlation among traits (Bryant, Combs & McCommas 1986; Bryant & Meffert 1988). Bryant and his co-workers interpreted their results as implying that predominantly non-additive components of genetic variation (V_D and V_I) affected the traits in the base population and that such non-additive components could be transformed into additive components during bottleneck episodes or founder events (Bryant, McCommas & Combs 1986; Bryant & Meffert 1988). Goodnight (1987, 1988) has shown explicitly how epistatic variance for quantitative traits in an ancestral population can be transformed into additive genetic variance in a derived bottleneck population. The levels of V_A can be several times higher than in the original population when there is epistasis. Bryant & Meffert (1988) discuss the, as yet limited, examples of epistasis influencing quantitative characters. In general, characters most closely related to fitness have low heritabilities (e.g. Falconer 1989), with non-additive genetic effects likely to be relatively important. The fate of genes influencing such characters is likely to be of particular consequence to continuing viability following a bottleneck.

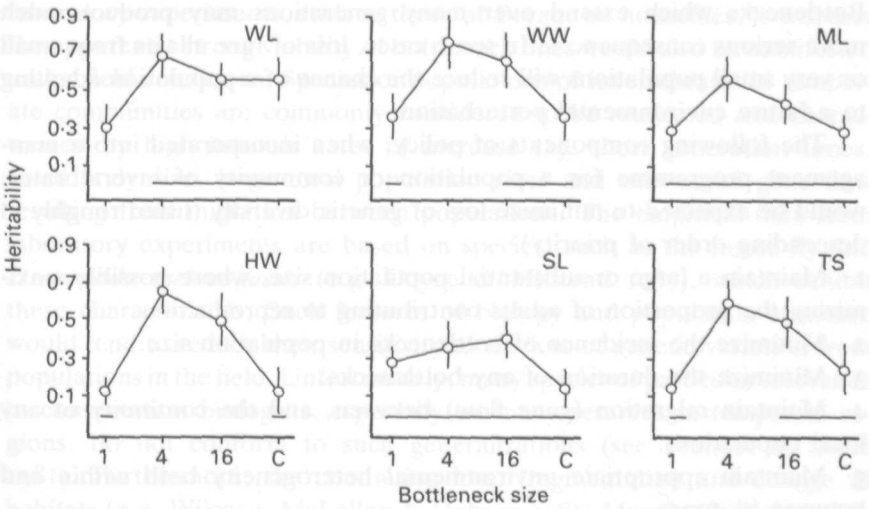

FIG. 3.10. Relationship between the size of the first bottleneck imposed on the experimental lines of the houseflies (see Fig. 3.8) and estimates of heritability made after the subsequent 'flush' period for six morphometric traits: WL, wing length; WW, wing width; ML, metafemur length; HW, head width; SW, scutellum width; TS, length of thoracic suture. If no underscore is present, the heritability differs significantly from that for the control, C (after Bryant, Combs & McCommas 1986).

CONCLUSIONS AND MANAGEMENT DESIGN

The results of Bryant's experiments on houseflies are of particular importance to conservation biologists in indicating that populations which have suffered bottlenecks in size, even extreme ones, may retain substantial potential for evolutionary adaptation. Interactions between genes are as yet comparatively poorly understood. The precise mechanisms involved in the phenomena described by Bryant are unclear, as are the relationships between the actual genetic systems and the statistical variance components. The existence of coadaptation between genes and of forms of non-additive genetic contributions to quantitative variation are likely to make variability within populations more resistant to loss than would be expected on the basis of theory developed largely from the perspective of genes acting independently from one another and in a purely additive manner (see Berry 1983).

Given that populations of invertebrates do not first become extinct for purely ecological reasons, novel patterns of genetic variation associated with a short bottleneck may provide potential for successful re-establishment and for adaptive responses to environmental change or perturbation.

Bottlenecks which extend over many generations may produce much more serious consequences. In some cases, loss of rare alleles from small or very small populations will reduce the chance of a population adapting to a future environmental perturbation.

The following components of policy, when incorporated into a management programme for a population or community of invertebrates, would be expected to minimize loss of genetic diversity (listed roughly in descending order of priority).

1 Maintain a large or substantial population size, where possible maximizing the proportion of adults contributing to reproduction.

2 Minimize the incidence of bottlenecks in population size.

3 Minimize the duration of any bottlenecks.

4 Maintain migration (gene flow) between, and the continuity of any local populations.

5 Maintain appropriate environmental heterogeneity both within and between biotopes.

In general, any such management programme which is successful in maintaining population sizes of the order of a few hundred individuals is unlikely to be unsuccessful because of loss of genetic variation. Even when effective numbers are consistently smaller than this, perhaps with intermittent short bottlenecks of ten or a few tens of breeding individuals, genetic variation is, in practice, almost always likely to be of less consequence to practicing conservationists than the likelihood of population extinction due to one of the many possible ecological or man-made causes (e.g. Murphy & Weiss 1988). In other words, because maximization of population size is of paramount concern to managers of natural populations of invertebrates wishing to minimize the chance of 'ecological extinction', it is in general not necessary to set up the maintenance of genetic variation as a specific major concern (see Berry 1983; Bryant, Meffert & McCommas 1990). Were the perspective of the conservationist to switch to a substantially longer time-scale, more specific emphasis on genetic variances and evolutionary potential would be necessitated.

Uncertainties of this type are not the only problem when attempting to apply the theory of population genetics and the insights of evolutionary genetics to practical objectives in conservation. As we have seen, although theory has been developed which predicts changes of genetic variance as a function of population structure and dynamics, and some empirical data describe such changes and their consequences in laboratory population cages, there are few direct data from natural populations which enable the theory to be applied with full confidence in conservation programmes. Thus, one concern with interpreting the significance of the results of

laboratory experiments, such as those of Bryant on houseflies, is whether the apparently strong viability of bottleneck lines would also be manifested under field conditions. Species or populations of invertebrates in temperate communities are commonly considered to be *r*-selected and characterized by high intrinsic rates of increase (r), short generation times, small body size, large total population sizes and substantial gene flow resulting from migration between populations. The empirical data from laboratory experiments are based on species, such as the house fly and *Drosophila melanogaster* (e.g. Coyne & Milstead 1987), which exhibit these characteristics. Such features of biology and population structure would tend to reduce their sensitivity to the loss of genetic variation from populations in the field. Unfortunately, many species of particular relevance to conservation biologists, especially on many reserves in temperate regions, do not conform to such generalizations (see Frankel & Soulé 1981). Furthermore, the continuing loss, fragmentation and change of habitats (e.g. Wilcove, McLellan & Dobson 1981; Murphy & Weiss 1988; Webb 1989) means that individual populations of many other species are increasingly beset by man-induced problems associated with isolation, small population size and environmental change. Longer-term monitoring of population dynamics and genetic variances in managed populations, and also experimental studies of more relevant laboratory systems are sorely needed. Studies of species relevant to conservationists, in which the relationships between ecological success and genetic diversity are examined for natural and laboratory populations established from different numbers of founders from a single source, would be especially exciting.

ACKNOWLEDGMENTS

I would like to thank E. H. Bryant for making his unpublished manuscripts available to me.

REFERENCES

Allendorf, F. W. (1983). Isolation, gene flow, and genetic differentiation among populations. *Genetics and Conservation: A Reference for Managing Wild Animal and Plant Populations* (Ed. by C. M. Schonewald-Cox, S. M. Chambers, B. MacBryde & W. L. Thomas), pp. 51–65. Benjamin Cummings Publishing Company, Menlo Park, California.

Allendorf, F. W. (1986). Genetic drift and the loss of alleles versus heterozygosity. *Zoo Biology*, **5**, 181–190.

Allendorf, F. W. & Leary, R. F. (1986). Heterozygosity and fitness in natural populations of animals. *Conservation Biology: Science of Diversity* (Ed. by M. E. Soulé), pp. 57–76. Sinauer Associates, Sunderland, Massachusetts.

Ayala, F. J. (1984). Molecular polymorphism: how much is there and why is there so much? *Developmental Genetics*, **4**, 379–391.

Bartlett, A. C. (1985). Guidelines for genetic diversity in laboratory colony establishment and maintenance. *Handbook of Insect Rearing* (Ed. by P. Singh & R. F. Moore), Vol. 1. Elsevier, Amsterdam.

Beardmore, J. A. (1983). Extinction, survival, and genetic variation. *Genetics and Conservation: A Reference for Managing Wild Animal and Plant Populations* (Ed. by C. M. Schonewald-Cox, S. M. Chambers, B. MacBryde & W. L. Thomas), pp. 125–151. Benjamin Cummings Publishing Company, Menlo Park, California.

Begon, M., Krimbas, C. B. & Loukas, M. (1980). The genetics of *Drosophila subobscura* populations. XV. Effective size of a natural population estimated by three independent methods. *Heredity*, **45**, 335–350.

Berry, R. J. (1971). Conservation aspects of the genetical constitution of populations. *The Scientific Management of Animal and Plant Communities for Conservation* (Ed. by E. Duffy & A. S. Watt), pp. 177–206. Blackwell Scientific Publications, Oxford.

Berry, R. J. (1983). Genetics and conservation. *Conservation in Perspective* (Ed. by A. Warren & F. B. Goldsmith), pp. 141–156. John Wiley & Sons, London.

Bishop, J. A. & Cook, L. M. (Eds) **(1981).** *Genetic Consequences of Man-Made Change*. Academic Press, London.

Bishop, J. A., Cook, L. M. & Muggleton, J. (1978). The response of two species of moths to industrialisation in northwest England. I. Polymorphism for melanism. *Philosophical Transactions of the Royal Society of London, Series B*, **281**, 489–515.

Black, W. C. IV, Ferrari, J. A., Rai, K. S. & Sprenger, D. (1988). Breeding structure of a colonising species: *Aedes albopictus* (Skuse) in the United States. *Heredity*, **60**, 173–181.

Boag, P. T. & van Noordwijk, A. J. (1987). Quantitative genetics. *Avian Genetics: A Population and Ecological Approach* (Ed. by F. Cooke & P. A. Buckley), pp. 45–78. Academic Press, London.

Brakefield, P. M. (1987). Industrial melanism: Do we have the answers? *Trends in Ecology & Evolution*, **2**, 117–122.

Brakefield, P. M. (1989). The variance in genetic diversity among subpopulations is more sensitive to founder effects or bottlenecks than is the mean: a case study. *Evolutionary Biology of Unstable Transient Populations* (Ed. by A. Fontdevila), pp. 145–161. Springer-Verlag, Berlin.

Brakefield, P. M. (1990). Genetic drift and patterns of diversity among colour-polymorphic populations of the Homopteran *Philaenus spumarius* in an island archipelago. *Biological Journal of the Linnean Society*, **39**, 219–237.

Brakefield, P. M. & Lees, D. R. (1987). Melanism in *Adalia* ladybirds and declining air pollution in Birmingham. *Heredity*, **59**, 273–277.

Brakefield, P. M. & Liebert, T. G. (1985). Studies of colour polymorphism in some marginal populations of the aposematic jersey tiger moth *Callimorpha quadripunctaria*. *Biological Journal of the Linnean Society*, **26**, 225–241.

Brussard, P. F. (1984). Geographic patterns and environmental gradients: the central-marginal model in *Drosophila* revisited. *Annual Review of Ecology and Systematics*, **15**, 25–64.

Bryant, E. H., Combs, L. M. & McCommas, S. A. (1986). Morphometric differentiation among experimental lines of the housefly in relation to a bottleneck. *Genetics*, **114**, 1213–1223.

Bryant, E. H., McCommas, S. A. & Combs, L. M. (1986). The effect of an experimental bottleneck upon quantitative genetic variation in the housefly. *Genetics*, **114**, 1191–1211.

Bryant, E. H. & Meffert, L. M. (1988). Effect of an experimental bottleneck on morphological integration in the housefly. *Evolution*, **42**, 698–707.

Bryant, E. H., Meffert, L. M. & McCommas, S. A. (1990). Fitness rebound in serially bottlenecked populations of the housefly. *American Naturalist* (in press).

Buri, P. (1956). Gene frequency in small populations of mutant *Drosophila*. *Evolution*, **10**, 367–402.

Cameron, R. A. D. & Dillon, P. J. (1984). Habitat stability, population histories and patterns of variation in *Cepaea*. *Malacologia*, **25**, 271–290.

Cavalli-Sforza, L. L. & Bodmer, W. F. (1971). *The Genetics of Human Populations*. Freeman, San Francisco.

Chakraborty, R. (1981). The distribution of the number of heterozygous loci in an individual in natural populations. *Genetics*, **98**, 461–466.

Chakraborty, R., Fuerst, P. A. & Nei, M. (1980). Statistical studies of protein polymorphism in natural populations. III. Allele frequency distributions. *Genetics*, **94**, 1029–1063.

Clarke, B. (1979). The evolution of genetic diversity. *Proceedings of the Royal Society of London, Series B*, **205**, 453–474.

Colgan, D. J. (1989). Developmental variation and allozymic polymorphism in the enzymes of glycolysis in grasshoppers. *Journal of Evolutionary Biology*, **2**, 141–151.

Cook, L. M., Mani, G. S & Varley, M. E. (1986). Postindustrial melanism in the peppered moth. *Science*, **231**, 611–613.

Coyne, J. A. & Milstead, B. (1987). Long-distance migration of *Drosophila*. 3. Dispersal of *D. melanogaster* alleles from a Maryland orchard. *American Naturalist*, **130**, 70–82.

Crow, J. F. & Kimura, M. (1970). *An Introduction to Population Genetics Theory*. Harper & Row, New York.

Davis, B. N. K. (1989). Habitat creation for butterflies on a landfill site. *The Entomologist*, **108**, 109–122.

Dempster, J. P., King, M. L. & Lakhani, K. H. (1976). The status of the swallowtail butterfly in Britain. *Ecological Entomology*, **1**, 71–84.

Dobzhansky, T. & Pavlovsky, O. (1957). An experimental study of interaction between genetic drift and natural selection. *Evolution*, **11**, 311–319.

Dover, G. A. (1986). Molecular drive in multigene families; how biological novelties arise, spread and are assimilated. *Trends in Genetics*, **2**, 159–165.

Eanes, W. F. (1987). Allozymes and fitness: evolution of a problem. *Trends in Ecology & Evolution*, **2**, 44–48.

Endler, J. A. (1986). *Natural Selection in the Wild*. Princeton University Press, Princeton, New Jersey.

Falconer, D. S. (1989). *Introduction to Quantitative Genetics*, 3rd edn. Longman, London.

Ford, E. B. (1975). *Ecological Genetics*, 4th edn. Chapman and Hall, London.

Frankel, O. H. & Soulé, M. E. (1981). *Conservation and Evolution*. Cambridge University Press, Cambridge.

Franklin, I. R. (1980). Evolutionary change in small populations. *Conservation Biology. An Evolutionary–Ecological Perspective* (Ed. by M. E. Soulé & B. A. Wilcox), pp. 135–149. Sinauer Associates, Sunderland, Massachusetts.

Fuerst, P. A. & Maruyama, T. (1986). Considerations on the conservation of alleles and of genic heterozygosity in small managed populations. *Zoo Biology*, **5**, 171–179.

Goodhart, C. B. (1973). A 16-year survey of *Cepaea* on the Hundred Foot Bank. *Malacologia*, **14**, 327–331.

Goodnight, C. J. (1987). On the effect of founder events on epistatic genetic variance. *Evolution*, **41**, 80–91.

Goodnight, C. J. (1988). Epistatsis and the effect of founder effects on the additive genetic variance. *Evolution*, **42**, 441–454.

Hanski, I. (1989). Metapopulation dynamics: Does it help to have more of the same? *Trends of Ecology & Evolution*, **4**, 113–114.

Harrison, S., Murphy, D. D. & Ehrlich, P. R. (1988). Distribution of the bay checkerspot butterfly, *Euphydryas editha bayensis*: evidence for a metapopulation model. *American Naturalist*, **132**, 360–382.

Hartl, D. L. (1980). *Principles of Population Genetics*. Sinauer Associates, Sunderland, Massachusetts.

Hedrick, P. W. (1986). Genetic polymorphism in heterogeneous environments: a decade later. *Annual Review of Ecology and Systematics*, **17**, 535–566.

Hedrick, P. W. (1989a). Genetic conservation in captive populations and endangered species. *Applied Population Biology* (Ed. by S. Jain & L. Botsford). Martinus Nijhoff/ W. Junk, Netherlands.

Hedrick, P. W. (1989b). Theoretical analysis of habitat selection and the maintenance of genetic variation. *The Evolution and Ecology of Drosophila* (Ed. by J. S. F. Barker & T. Starmer). Plenum, London.

Hedrick, P. W., Brussard, P. F., Allendorf, F. W., Beardmore, J. A. & Orzack, S. (1986). Protein variation, fitness and captive propagation. *Zoo Biology*, **5**, 91–99.

Hewitt, G. M. (1988). Hybrid zones: natural laboratories for evolutionary studies. *Trends in Ecology & Evolution*, **3**, 158–167.

Hoekstra, R. F. (1975). A deterministic model of cyclical selection. *Genetical Research, Cambridge*, **25**, 1–15.

James, J. W. (1971). The founder effect and response to artificial selection. *Genetical Research, Cambridge*, **16**, 241–250.

Janson, K. (1987). Genetic drift in small and recently founded populations of the marine snail *Littorina saxatalis*. *Heredity*, **58**, 31–37.

Kettlewell, H. B. D. (1973). *The Evolution of Melanism*. Clarendon Press, Oxford.

Klarenberg, A. J., Vermeulen, J. W. C., Jacobs, P. J. M. & Scharloo, W. (1988). Genetic and dietary regulation of tissue-specific expression of α-amylase in *Drosophila melanogaster*. *Comparative Biochemistry & Physiology*, *B*, **89B**, 143–146.

Koenig, W. D. & Albano, S. S. (1987). Lifetime reproductive success, selection, and the opportunity for selection in the white-tailed skimmer *Plathemis lydia* (Odonata: Libellulidae). *Evolution*, **41**, 22–36.

Kreitman, M. E. & Aguadé, M. (1986). Excess polymorphism at the Adh locus in *Drosophila melanogaster*. *Genetics*, **114**, 93–110.

Lande, R. (1980). Genetic variation and phenotypic evolution during allopatric speciation. *American Naturalist*, **116**, 463–479.

Lande, R. (1981). The minimum number of genes contributing to quantitative variation between and within populations. *Genetics*, **99**, 541–553.

Lande, R. & Arnold, S. J. (1983). The measurement of selection on correlated characters. *Evolution*, **37**, 1210–1226.

Lande, R. & Barrowclough, G. F. (1987). Effective population size, genetic variation, and their use in population management. *Viable Populations for Conservation* (Ed. by M. E. Soulé), pp. 87–123. Cambridge University Press, Cambridge.

Lawrence, M. J. (1984). The genetical analysis of ecological traits. *Evolutionary Ecology* (Ed. by B. Shorrocks), pp. 27–63. Blackwell Scientific Publications, Oxford.

Lees, D. R. (1981). Industrial melanism: genetic adaptation of animals to air pollution. *Genetic Consequences of Man-Made Change* (Ed. by J. A. Bishop & L. M. Cook), pp. 129–176. Academic Press, London.

Levins, R. (1970). Extinction. *Some Mathematical Questions in Biology*, pp. 13–34. American Mathematical Society, Providence, R. I.

Lewontin, R. C. (1974). *The Genetic Basis of Evolutionary Change*. Columbia University Press, New York.

Liebert, T. G. & Brakefield, P. M. (1990). The genetics of colour polymorphism in the aposematic jersey tiger moth *Callimorpha quadripunctaria*. *Heredity*, **64**, 87–92.

Mather, K. (1982). Response to selection. *The Genetics and Biology of Drosophila, Vol 3c* (Ed. by M. Ashburner & J. N. Thompson). Academic Press, London.

McKechnie, S. W., Ehrlich, P. R. & White, R. R. (1975). Population genetics of *Euphydryas* butterflies. I. Genetic variation and the neutrality hypothesis. *Genetics*, **81**, 571–594.

Mueller, L. E., Wilcox, B. A., Ehrlich, P. R. & Murphy, D. D. (1985). A direct assessment of the role of genetic drift in determining allele frequency variation in populations of *Euphydryas editha*. *Genetics*, **110**, 495–511.

Murphy, D. D. & Weiss, S. B. (1988). Ecological studies and the conservation of the Bay Checkerspot butterfly, *Euphydryas editha bayensis*. *Biological Conservation*, **46**, 183–200.

Myers, J. H. & Sabath, M. D. (1981). Genetic and phenotypic variability, genetic variance, and the success of establishment of insect introductions for the biological control of weeds. *Proceedings, V. International Symposium on the Biological Control of Weeds, Brisbane* (Ed. by E. S. Delfosse), pp. 91–102. CSIRO, Canberra, Australia.

Nei, M. (1977). *F*-statistics and analysis of gene diversity in subdivided populations. *Annals of Human Genetics*, **41**, 225–233.

Nei, M. (1986). Definition and estimation of fixation indices. *Evolution*, **40**, 643–645.

Nei, M. (1987). *Molecular Evolutionary Genetics*. Columbia University Press, New York.

Nei, M., Maruyama, T. & Chakraborty, R. (1975). The bottleneck effect and genetic variability in populations. *Evolution*, **29**, 1–10.

Nevo, E. (1978). Genetic variation in natural populations: patterns and theory. *Theoretical Population Biology*, **13**, 121–177.

Nevo, E., Beiles, A. & Ben-Shlomo, R. (1984). The evolutionary significance of genetic diversity: Ecological, demographic and life history correlates. *Evolutionary Dynamics of Genetic Diversity. Lecture Notes in Biomathematics* 53 (Ed. by G. S. Mani), pp. 13–213. Springer-Verlag, New York.

Oates, M. R. & Warren, M. S. (1989). *A review of butterfly introductions in Britain and Ireland*. Research & Survey of Conservation Series, Nature Conservancy Council, Peterborough.

Oxford, G. S. (1975). Food-induced esterase phenocopies in the snail *Cepaea nemoralis*. *Heredity*, **35**, 361–370.

Oxford, G. S. (1989). Genetics and distribution of black spotting in *Enoplognatha ovata* (Araneae: Theridiidae), and the role of intermittent drift in population differentiation. *Biological Journal of the Linnean Society*, **36**, 111–128.

Oxford, G. S. & Shaw, M. W. (1986). Long-term variation in colour-morph frequencies in the spider *Enoplognatha ovata* (Clerck) (Araneae: Theridiidae): natural selection, migration and intermittent drift. *Biological Journal of the Linnean Society*, **27**, 225–249.

Parkin, D. T. (1979). *An Introduction to Evolutionary Genetics*. Edward Arnold, London.

Pimm, S. L., Jones, H. L. & Diamond, J. (1988). On the risk of extinction. *American Naturalist*, **132**, 757–785.

Pollak, E. (1983). A new method for estimating the effective population size from allele frequency changes. *Genetics*, **104**, 531–548.

Powell, J. R. (1975). Protein variation in natural populations of animals. *Evolutionary Biology*, **8**, 79–119.

Quinn, J. F. & Hastings, A. (1987). Extinction in subdivided populations. *Conservation Biology*, **1**, 198–208.

Quinn, T. W. & White, B. N. (1987). Analysis of DNA sequence variation. *Avian Genetics: A Population and Ecological Approach* (Ed. by F. Cooke & P. A. Buckley), pp. 163–198. Academic Press, London.

Rich, S. S., Bell, A. E. & Wilson, S. P. (1979). Genetic drift in small populations of *Tribolium*. *Evolution*, **33**, 579–584.

Robertson, A. (1960). A theory of limits in artificial selection. *Proceedings of the Royal Society of London, Series B*, **153**, 234–249.

Rockwell, R. F. & Barrowclough, G. F. (1987). Gene flow and the genetic structure of populations. *Avian Genetics: A Population and Ecological Approach* (Ed. by F. Cooke & P. A. Buckley), pp. 223–255. Academic Press, London.

Santos, M., Ruiz, A. & Fontdevila, A. (1989). The evolutionary history of *Drosophila buzzatii*. XIII. Random differentiation as a partial explanation of chromosomal variation in a structured natural population. *American Naturalist*, **133**, 183–197.

Schonewald-Cox, C. M., Chambers, S. M., MacBryde, B. & Thomas, W. L. (Eds) **(1983).** *Genetics and Conservation: A Reference for Managing Wild Animal and Plant Populations*. Benjamin Cummings Publishing Company, Menlo Park, California.

Selander, R. K. (1976). Genic variation in natural populations. *Molecular Evolution* (Ed. by F. Ayala), pp. 21–45. Sinauer Associates, Sunderland, Massachusetts.

Singer, M. C., Ng, D. & Thomas, C. D. (1988). Heritability of oviposition preference and its relationship to offspring performance within a single insect population. *Evolution*, **42**, 977–985.

Slatkin, M. (1985). Gene flow in natural populations. *Annual Review of Ecology and Systematics*, **16**, 393–430.

Slatkin, M. (1987). Gene flow and the geographic structure of natural populations. *Science*, **236**, 787–792.

Soulé, M. E. (1980). Thresholds for survival: maintaining fitness and evolutionary potential. *Conservation Biology. An Evolutionary–Ecological Perspective* (Ed. by M. E. Soulé & B. A. Wilcox), pp. 151–169. Sinauer Associates, Sunderland, Massachusetts.

Soulé, M. E. (Ed.) **(1986).** *Conservation Biology: Science of Scarcity and Diversity*. Sinauer Associates, Sunderland, Massachusetts.

Soulé, M. E. (Ed.) **(1987).** *Viable Populations for Conservation*. Cambridge University Press, Cambridge.

Soulé, M., Gilpin, M., Conway, W. & Foose, T. (1986). The millenium ark: How long a voyage, how many staterooms, how many passengers? *Zoo Biology*, **5**, 101–113.

Soulé, M. E. & Wilcox, B. A. (Eds) **(1980).** *Conservation Biology. An Evolutionary-Ecological Perspective*. Sinauer Associates, Sunderland, Massachusetts.

Templeton, A. R. (1986). Coadaptation and outbreeding depression. *Conservation Biology: Science of Scarcity and Diversity* (Ed. by M. E. Soulé), pp. 105–116. Sinauer Associates, Sunderland, Massachusetts.

Thomas, J. A. (1983a). The ecology and conservation of *Lysandra bellargus* (Lepidoptera: Lycaenidae) in Britain. *Journal of Applied Ecology*, **20**, 59–83.

Thomas, J. A. (1983b). The ecology and status of *Thymelicus acteon* (Lepidoptera: Hesperiidae) in Britain. *Ecological Entomology*, **8**, 427–435.

Turner, J. R. G. (1984). Mimicry: the palatability spectrum and its consequences. *Symposium of the Royal Entomological Society of London*, **11**, 141–161.

Van Delden, W. (1982). The alcohol dehydrogenase polymorphism in *Drosophila melanogaster*: selection at an enzyme locus. *Evolutionary Biology*, **15**, 187–222.

Via, S. (1984). The quantitative genetics of polyphagy in an insect herbivore. I. Genotype–environment interaction in larval performance on different host plant species. *Evolution*, **38**, 881–895.

Via, S. (1986). Genetic covariance between oviposition preference and larval performance in an insect herbivore. *Evolution*, **40**, 778–785.

Via, S. & Lande, R. (1985). Genotype–environment interaction and the evolution of phenotypic plasticity. *Evolution*, **39**, 505–522.

Wade, M. J. & McCauley, D. E. (1988). Extinction and recolonization: their effects on the genetic differentiation of local populations. *Evolution*, **42**, 995–1005.

Warren, M. S. (1987a). The ecology and conservation of the heath fritillary butterfly, *Mellicta athalia*. III. Population dynamics and the effect of habitat management. *Journal of Applied Ecology*, **24**, 499–513.

Warren, M. S. (1987b). The ecology and conservation of the heath fritillary butterfly, *Mellicta athalia*. II. Adult population structure and mobility. *Journal of Applied Ecology*, **24**, 483–498.

Watt, W. B. (1977). Adaptation at specific loci. I. Natural selection on phosphoglucose isomerase of *Colias* butterflies: biochemical and population aspects. *Genetics*, **87**, 177–194.

Watt, W. B., Cassin, R. C. & Swan, M. S. (1983). Adaptation at specific loci. III. Field behaviour and survivorship differences among *Colias* PGI genotypes are predictable from *in vitro* biochemistry. *Genetics*, **103**, 725–739.

Watt, W. B., Carter, P. A. & Blower, S. M. (1985). Adaptation at specific loci. IV. Differential mating success among glycolytic allozyme genotypes of *Colias* butterflies. *Genetics*, **109**, 157–175.

Webb, N. R. (1989). Studies on the invertebrate fauna of fragmented heathland in Dorset, UK, and the implications for conservation. *Biological Conservation*, **47**, 153–165.

Wilcove, D. S., McLellan, C. H. & Dobson, A. P. (1981). Habitat fragmentation in the temperate zone. *Conservation and Evolution* (Ed. by O. H. Frankel & M. E. Soulé), pp. 237–256. Cambridge University Press, Cambridge.

Wolda, H. (1969). Fine distribution of morph frequencies in the snail, *Cepaea nemoralis* near Groningen. *Journal of Animal Ecology*, **38**, 305–327.

Wool, D. (1987). Differentiation of island populations: a laboratory model. *American Naturalist*, **129**, 188–202.

Wright, S. (1931). Evolution in Mendelian populations. *Genetics*, **16**, 97–159.

Wright, S. (1943). Isolation by distance. *Genetics*, **28**, 114–138.

Wright, S. (1951). The genetical structure of populations. *Annals of Eugenics*, **15**, 323–354.