Example 2.4

Sickle-cell anaemia in man is a well-known example of heterozygote advantage. It is particularly useful as an example because the data allow a test of observation with theory. The disease is caused by the abnormal haemoglobin-S. Homozygotes suffer from a severe anaemia from which many die, yet the gene is present among Africans and their descendants in America at frequencies much too high to be accounted for by mutation counterbalancing the selection against homozygotes. The explanation of the high frequencies is that heterozygotes have an advantage over normal homozygotes through an increased resistance to malaria (Allison, 1954). The selective forces can be calculated from data given by Allison (1956) and one can then see how well these can account for the observed gene frequency. Allison classified 287 infants and 654 adults, from a district of Tanzania, for genotype. (Homozygotes are recognized by the presence of red blood cells with a characteristic 'sickle' shape; heterozygotes are recognized by the sickling of their cells when the blood sample is deoxygenated.) The observed numbers and frequencies are shown in the table, with the gene frequencies calculated from them by equation [1.1]. (AA denotes the normal homozygote, AS the heterozygote, and SS the anaemic homozygote.) Most of the differential selection is thought to take place before adulthood, i.e., the surviving genotypes do not differ much in fertility. The infants therefore represent the genotype frequencies before selection and the adults after selection, and so we can calculate the selection coefficients from the observed frequencies. First, however, note that if the gene frequency is in equilibrium it will be the same after selection as it was before, and the data agree well with this expectation. Dividing the frequency of each genotype after selection by its frequency before selection gives the relative fitness of that genotype, as shown in the table. The fitnesses of the homozygotes can then be expressed relative to the heterozygote by dividing each by the heterozygote fitness. The homozygote fitnesses are $1 - s_1$ and $1 - s_2$, from which the selection coefficients work out to be 0.24 against AA and 0.80 against SS, both relative to AS. The equilibrium gene frequency expected to result from this selection against both homozygotes, by equation [2.19], is $q_s = 0.23$, which is reasonably close to the observed value. Thus the selective forces observed in the differential viability do satisfactorily account for the frequency of the sickle-cell gene in this population.

	Genotype AA	AS	SS	*Frequency of S-gene*
Numbers of infants	189	89	9	
adults	400	249	5	
Frequency in infants	0.6585	0.3101	0.0314	0.1864
adults	0.6116	0.3807	0.0076	0.1980
Relative fitness	0.9288	1.2277	0.2420	
Fitness relative to AS	0.7565	1	0.1971	
Selection coefficient	$s_1 = 0.2435$		$s_2 = 0.8029$	

$$\text{Expected } q_s = \frac{s_1}{s_1 + s_2} = 0.2327$$

The selective values may be more interesting if expressed relative to the normal homozygote. The fitness of AS is then $1/(1 - s_1) = 1.32$, and that of SS is $(1 - s_2)/(1 - s_1) = 0.26$. Thus the resistance to malaria confers a 32 per cent advantage on the heterozygote, and this balances a 74 per cent disadvantage in the anaemic homozygote when the gene frequency is about 0.2.

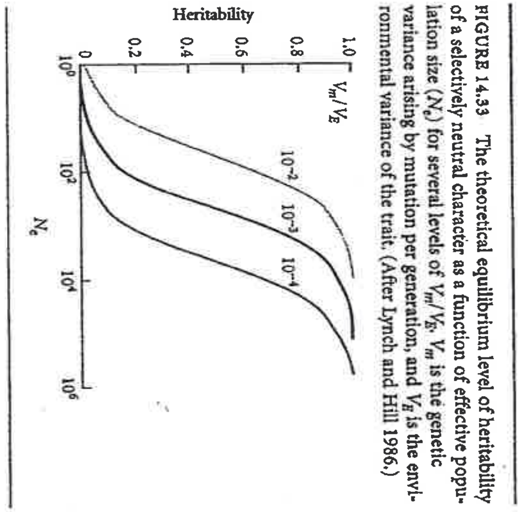


FIGURE 14.33 The theoretical equilibrium level of heritability of a selectively neutral character as a function of effective population size (N_e) for several levels of V_m/V_E. V_m is the genetic variance arising by mutation per generation, and V_E is the environmental variance of the trait. (After Lynch and Hill 1986.)

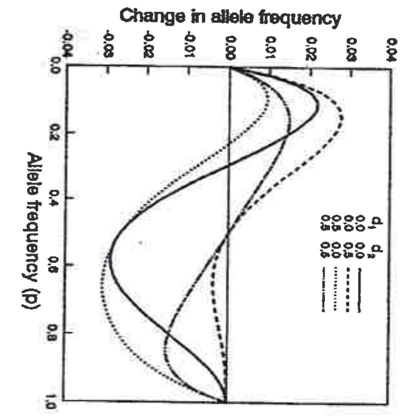
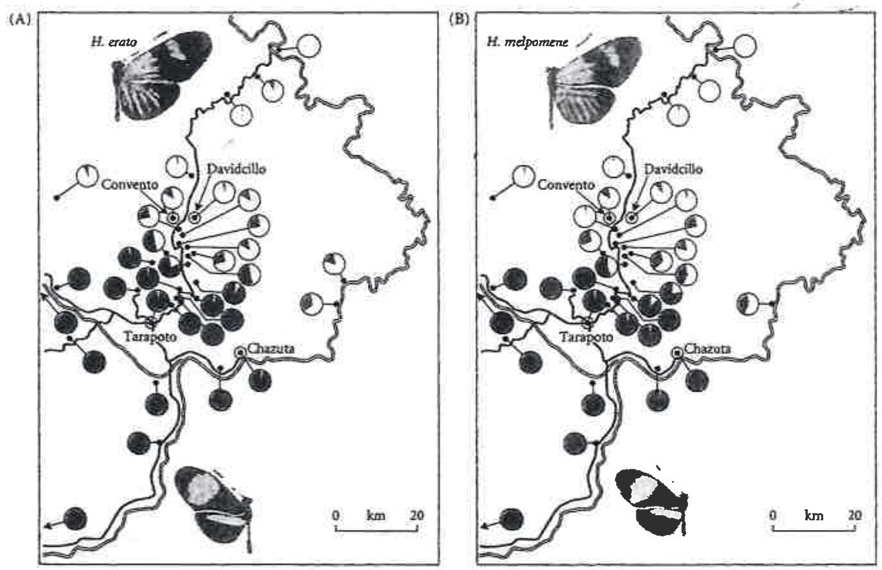
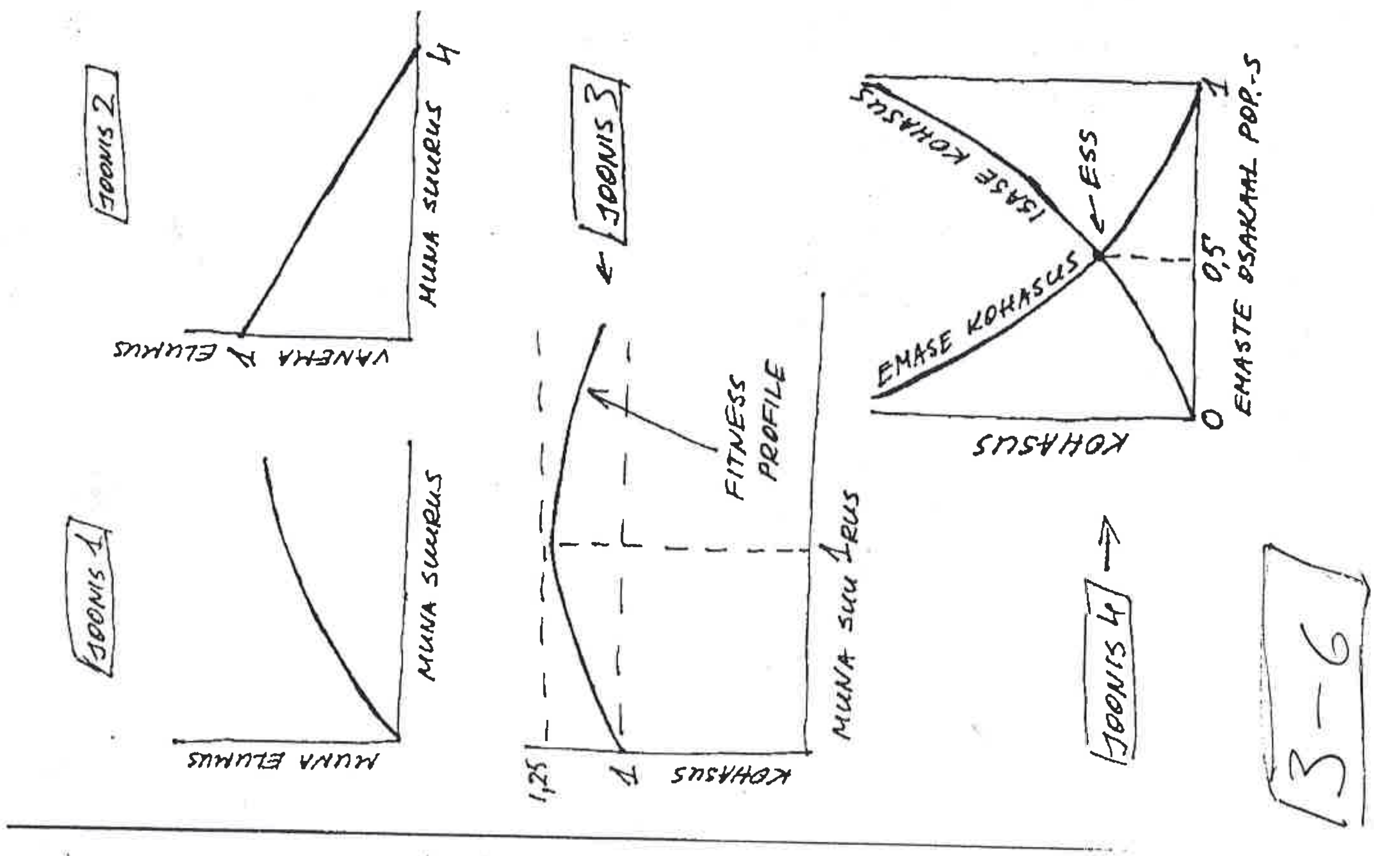


Figure 9.10 The change in allele frequency for the frequency-dependent model described in Table 9.15. In all cases, $s = 0.5$.

FIGURE 13.27 The proportions of two color forms of the butterfly *Heliconius erato* (A) at various sites in a small region of Peru, and of the almost identical color forms of *H. melpomene* (B) at the same sites. These species are Müllerian mimics. In both species, almost complete replacement of one color form by the other occurs over a very short distance. The four named localities are those at which Mallet and Barton obtained *H. erato* for the transfer experiment described in the text. (After Mallet and Barton 1989.)





3-7

Taimede elustrateegiate jaotusi

McArthuri ja Wilsoni järgi	*K*-strateegia		*r*-strateegia
Grime'i järgi	*C* — konkurentsi- (tugevad) taimed	*S* — stressi- (kindlad) taimed	*R* — ruderaal- taimed
Ramenski järgi	violendid (rõhujad)	patiendid (talujad)	eksplerendid (kohatäitjad)
Keskkond	pidevalt soodus	pidevalt ebasoodus	muutlik, lühiajaliselt soodus
Taime reageerimine keskkonnahälbeile	juurdekasvu muutused	erilised kohastu- mused, aastarütm	lühike eluiga, seemnevaru
Kasv ja uuenemine	tugev kasv, pikk eluiga, harv seemneline uuenemine	nõrk kasv, pikk eluiga, valdavalt vegetatiivne uuenemine	kiire kasv soodsail perioodidel, rikkalik seemneline uuenemine
Populatsiooni arvu- kus ja regulatsioon	stabiilne, reguleerub koosluse sees tiheduse kaudu	stabiilne, reguleerub keskkonnategurite mõjul	kõikuv: madal kuni ülikõrge
Näiteid Eesti taim- kattest	tamm, kuusk jt. kliimaks- koosluste edifikaatorid, kõrvenõges, kerahein	kuivustaimed, raba- taimed, varjutaimed	umbrohud, ajutiste veekogude taimed