

TABLE 2.3 Values of the coefficient of relatedness (r_{ij}) for different relationships

Relationship	r_{ij}
Self and monozygotic (identical) twins	1.0
Parents and offspring	0.5
Grandparents and offspring	0.25
Full siblings	0.5
Half siblings	0.25
Aunt or uncle to niece or nephew	0.25
First cousins	0.125

individual's genes come from each parent. The value of r_{ij} for full-siblings is also 0.5, but only on average, because each sibling received half of their genes from each of the same pair of parents, but the haploid set of genes that is put in each parental gamete is a random sample of half the parental genome due to recombination. More distant coefficients of relatedness can be calculated as products. For example, because parents and offspring share half their genes, the r_{ij} for grandparents and offspring is the product of the two coefficients ($0.5 \times 0.5 = 0.25$). Table 2.3 gives values of the coefficient of relatedness for a variety of different relationships.

Dole and Ritland (1993) estimated F using seven allozyme loci in natural populations of two species of monkey flower. *Mimulus guttatus* is primarily **outcrossing** (outbreeding), while *M. platycalyx* is primarily selfing (Figure 2.15). As expected, F was much higher in the latter, averaging 0.54 compared to an average F of 0.17 for *M. guttatus*.

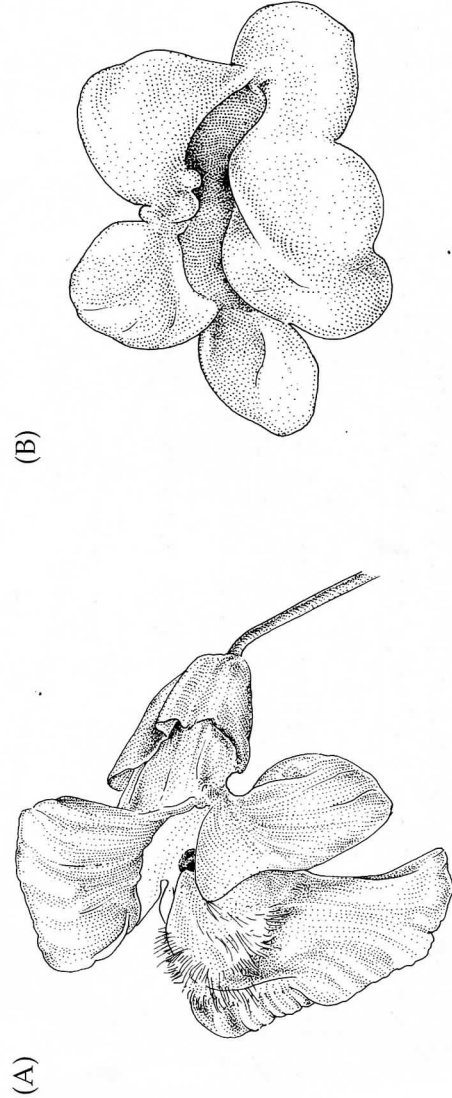


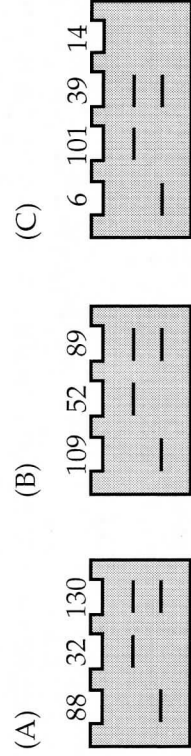
Figure 2.15 Flowers of (A) *Mimulus guttatus* and (B) *M. platycalyx*.

Inbreeding can also be estimated and studied directly using pedigrees. This approach is very useful if detailed pedigrees are known for the study organism, but this information is rarely available in natural populations, especially since paternity can often be uncertain. Pedigree analysis is described in detail in the population genetics books listed in the Suggested Readings at the end of this chapter.

The most important effect of the genome-wide increase in homozygosity caused by inbreeding is called **inbreeding depression**, which refers to a decrease in fitness that often accompanies inbreeding. Inbreeding and inbreeding depression are important in a number of contexts, and therefore will be discussed further in later chapters.

PROBLEMS

Whenever a statistical test is needed, report the test statistic (e.g., value of chi-square), the P -value and explain what the statistical result means biologically. The following electrophoresis gel diagrams are used in Problems 2.3 and 2.5. Above each lane is the number of individuals in the population sample with the banding pattern illustrated.



2.1 Spitze (1993) reported the following numbers of genotypes at the *PGI* locus in the *Daphnia* population in Nothing Pond:

SS	11
SS-	55
S-S-	61

- What are the observed genotype and allele frequencies?
 - Given the observed allele frequencies, what are the genotypic frequencies expected under Hardy-Weinberg? Using a chi-square test, how well do the observed genotypic frequencies agree with the Hardy-Weinberg expectations?
- 2.2 Calculate F for the *Daphnia PGI* locus in the Ojibway Pond (page 35; note that there are data for *PGM* in the text as well) and the Nothing Pond (Problem 2.1 above) populations. What is a possible biological interpretation of these data? Explain your reasoning.

2.3 Gels A and B show banding patterns from RFLP markers in two related plant species.

- Estimate allele and genotypic frequencies and test for HWE in each species.
- Estimate F for each species.
- What is a possible biological interpretation of the data from parts a and b? Explain your reasoning.

2.4 RAPD and AFLP markers have only two genotypes—presence or absence of a band. When a band is present, the genotype can be homozygous or heterozygous. Therefore, only the band-absent (null) genotype can be scored definitively. In a study of a selfing plant (*Medicago truncatula*), Bonnin et al. (1996) reported band-presence at a frequency of 0.59 at their RAPD locus B6-600 in a population from Aude, France.

- Assuming HWE, what are the frequencies of the two alleles and the three genotypes?
- Because this is a selfing plant, assume HWE is not valid. Is your estimate of the frequency of the band-present allele an over- or underestimate? Explain your reasoning.

2.5 Gel C shows the banding patterns from two AFLP markers (the upper and lower sets of bands).

- Estimate the frequency q of the null allele of each of the two AFLP markers assuming HWE.
- Estimate the percentage of *band-present* individuals (not the overall frequencies) that are heterozygous at each of the two markers. What biological principle does the difference between these two percentages illustrate?

SUGGESTED READINGS

- Awise, J. C. 1994. *Molecular Markers, Natural History, and Evolution*. Chapman and Hall, New York. A review of many ways that molecular markers can be used to study natural populations.
- Hartl, D. L. 2000. *A Primer of Population Genetics*, 3rd Edition. Sinauer Associates, Sunderland, MA. A more mathematical introduction to the field.
- Hartl, D. L., and A. G. Clark. 1997. *Principles of Population Genetics*, 3rd Edition. Sinauer Associates, Sunderland, MA. A detailed and comprehensive treatment of population genetics.

CHAPTER REFERENCES

- Barrett, S. C. H. 1988. The evolution, maintenance, and loss of self-incompatibility systems. Pp. 98–124 in J. L. Doust, and L. L. Doust, eds. *Plant Reproductive Ecology*. Oxford University Press, New York.

- Bonnin, I., T. Huguet, M. Gherardi, J.-M. Prosperi, and I. Olivieri. 1996. High level of polymorphism and spatial structure in a selfing plant species, *Medicago truncatula* (Leguminosae), shown using RAPD markers. *Am. J. of Botany* 83:843–855.
- Crespi, B. J. 1989. Causes of assortative mating in arthropods. *Anim. Behav.* 38:980–1000.
- Dole, J., and K. Ritland. 1993. Inbreeding depression in two *Mimulus* taxa measured by multigenerational changes in the inbreeding coefficient. *Evolution* 47:361–373.
- Hardy, G. 1908. Mendelian proportions in a mixed population. *Science* 28: 49–50.
- Hillis, D. M., C. Moritz, and B. K. Mable. 1996. *Molecular Systematics*, 2nd Edition. Sinauer Associates, Sunderland, MA.
- Keller, L. F., and D. M. Waller. 2002. Inbreeding effects in wild populations. *Trends in Ecology and Evolution* 17:230–241.
- Kettlewell, H. B. D. 1956. Further selection experiments on industrial melanism in the *Lepidoptera*. *Heredity* 10:287–301.
- Lewontin, R. C., and J. L. Hubby. 1966. A molecular approach to the study of genic heterozygosity in natural populations. II. Amount of variation and degree of heterozygosity in natural populations of *Drosophila pseudoobscura*. *Genetics* 54: 595–609.
- Majerus, M. E. N. 1998. *Melanism: Evolution in Action*. Oxford University Press, New York.
- Maynard Smith, J. 1998. *Evolutionary Genetics*. Oxford University Press, New York.
- Mueller, U. G., and L. L. Wolfenbarger. 1999. AFLP genotyping and fingerprinting. *Trends in Ecology and Evolution* 14:389–394.
- Murphy, R. W., J. W. Sites, Jr., D. G. Buth, and C. H. Haufler. 1996. Proteins: Isozyme electrophoresis. Pp. 45–126 in D. M. Hillis, C. Moritz, and B. K. Mable, eds. *Molecular Systematics*, 2nd Edition. Sinauer Associates, Sunderland, MA.
- Parker, P. G., A. A. Snow, M. D. Schug, G. C. Booton, and P. A. Fuerst. 1998. What molecules can tell us about populations: Choosing and using a molecular marker. *Ecology* 79:361–382.
- Spitze, K. 1993. Population structure in *Daphnia obtusa*—quantitative genetic and allozymic variation. *Genetics* 135:367–374.
- Sunnucks, P. 2000. Efficient genetic markers for population biology. *Trends in Ecology and Evolution* 15:199–203.
- Templeton, A. R., and B. Read. 1994. Inbreeding: One word, several meanings, much confusion. Pp. 91–105 in V. Loeschke, J. Tomiuk, and S. K. Jain, eds. *Conservation Genetics*. Birkhauser Verlag, Basel, Switzerland.
- Waser, N. M. 1993. Population structure, optimal outbreeding, and assortative mating in angiosperms. Pp. 173–199 in N. Thornhill, ed. *The Natural History of Inbreeding and Outbreeding*. University of Chicago Press, Chicago.
- Weinberg, W. 1908. On the demonstration of heredity in man. *Naturkunde in Wurttemberg Stuttgart*. 64: 368–382. [Original in German. Translated in S. H. Boyer IV (ed.), 1963, "Papers on Human Genetics," Prentice Hall, Englewood Cliffs, NJ.]
- Whitlock, M. C. 1992. Nonequilibrium population structure in forked fungus beetles: Extinction, colonization, and the genetic variance among populations. *Am. Nat.* 139:952–970.
- Williams, J. G. K., A. R. Kubelik, K. J. Livak, J. A. Rafalski, and S. V. Tingey. 1990. DNA polymorphisms amplified by arbitrary primers are useful as genetic markers. *Nucleic Acids Research* 18:6531–6535.