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INTRODUCTION TO CONSERVATION GENETICS

CAMBRIDGE

Introduction to Conservation Genetics

Second Edition

Richard Frankham

Macquarie University and The Australian Museum, Sydney

Jonathan D. Ballou

Smithsonian Institution, Washington, DC

David A. Briscoe

Macquarie University, Sydney

Line drawings by

Karina H. McInnes

Melbourne

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Diversification among fragments in the means for quantitative characters increases with generations in a manner similar to allele frequencies (Fig. 14.7). Since we cannot distinguish the individual loci and follow their allelic frequencies, changes in additive genetic variances are measured. Additive genetic variation (V_A) among fragments increases and that within populations decreases in parallel with heterozygosity. For additive loci (no dominance) the genetic variance among populations increases to $2FV_A$, whilst the genetic variance within populations decreases to $V_A(1 - F)$ (Falconer & Mackay 1996). With dominance the situation is more complex. However, the genetic variation among populations increases with F , while the variation within populations may increase initially with F , before declining to zero at high values of F (Van Buskirk & Willi 2006).

Each of the many loci affecting a quantitative character undergoes drift independently. Some attain fixation, while others remain polymorphic. The combined effect across all loci in the genome will closely reflect the average effects we have defined above (Table 14.2), i.e. an overall reduction in heterozygosity. However, replicate populations from the same initial base population will have diverse genetic constitutions, as they will vary in the alleles fixed, and in the loci still polymorphic.

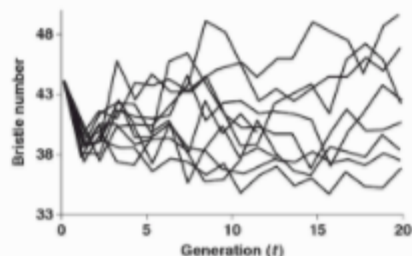


Fig. 14.7 Random genetic drift for abdominal bristle number in fruit flies (after Falconer & Mackay 1996, based on Rasmuson). Mean bristle number across generations in 10 populations, all founded from the same base population, and reproduced from a single pair of parents in each generation (two populations became extinct). Means drift over generations for individual populations and divergence among population means generally increases with generations.

Measuring population fragmentation: F statistics

Sewall Wright (Wright 1969) partitioned inbreeding in the total (T) population (F_{IT}) into:

- inbreeding of individuals relative to their sub-population (S) or fragment, F_{IS} , and
- inbreeding due to differentiation among sub-populations, relative

Quantitative characters exhibit diversification in population means due to genetic drift.

The degree of differentiation among fragments can be described by partitioning the overall inbreeding into components within and among

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David A.

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F_{IT} , F_{IS} and F_{ST} are referred to as F statistics (Wright 1969). F_{IS} is the inbreeding coefficient, F (Chapter 12), averaged across all individuals from all population fragments. F_{ST} (referred to as G_{ST} for multi-allelic loci) is the effect of population subdivision on inbreeding. For a locus with two alleles, F_{ST} is defined as

$$F_{ST} = \frac{\sigma_p^2}{p(1-p)} \tag{14.3}$$

where $\bar{p}$ is the mean frequency of allele and σ_p^2 is the variance in frequency of allele A_1 over sub-populations. When all sub-populations have the same allele frequencies, both σ_p^2 and F_{ST} are zero. If the variance is at its binomial maximum $p(1-p)$, then $F_{ST} = 1$. Thus, F_{ST} has a range from 0 (no differentiation among fragments) to 1 (fixation of different alleles in fragments) for loci with two alleles. Note that $\sigma_q^2 = \sigma_p^2$.

F statistics can be calculated using Equation 12.9 which relates heterozygosity and inbreeding. This allows F statistics to be determined from heterozygosity for genetic markers using the following equations (Nei 1987):

$$F_{IS} = 1 - \frac{H_I}{H_S} \tag{14.4}$$

$$F_{ST} = 1 - \frac{H_S}{H_T} \tag{14.5}$$

$$F_{IT} = 1 - \frac{H_I}{H_T} \tag{14.6}$$

where H_I is the observed heterozygosity averaged across all population fragments, H_S is the expected heterozygosity averaged across all population fragments and H_T is the expected heterozygosity for all populations, treated as a whole (equivalent to H_d).

Table 14.3 illustrates the application of F statistics using hypothetical examples. Case (A) shows two population fragments with identical allele frequencies, but with inbreeding in fragment 2. F_{IS} is therefore greater than zero. When allelic frequencies are very similar in different fragments, as would be the case when migration is high, or the populations have only recently fragmented, then divergence is low and $H_S \sim H_T$, and $F_{ST} \sim 0$. In (B) there is no inbreeding within either population fragment. The observed heterozygosity is equal to the expected heterozygosity ($H_I = H_S$), and $F_{IS} = 0$. However, the population fragments have different allele frequencies, as will occur with severely restricted gene flow. H_T exceeds H_S , and $F_{ST} > 0$. In (C) there is both divergence in allele frequencies and inbreeding, F_{IS} and F_{ST} are greater than zero and the total inbreeding, F_{IT} , reflects both effects (Equation 14.6).

Calculation of F statistics based on heterozygosities in the endangered Pacific yew in western North America (Example 14.4) reveals inbreeding within populations ($F_{IS} > 0$) and differentiation among populations ($F_{ST} > 0$).

Table 14.3. Hypothetical examples demonstrating calculation of *F* statistics from genotype data

	Genotypes			Allele frequency	<i>F</i>	<i>H_e</i> (= 2 <i>pq</i>)
Population	<i>A</i> ₁ <i>A</i> ₁	<i>A</i> ₁ <i>A</i> ₂	<i>A</i> ₂ <i>A</i> ₂			
(A) Populations with same allele frequencies, one random mating, other inbreeding						
1	0.25	0.5	0.25	<i>p</i> = 0.5 <i>q</i> = 0.5	0	0.5
2	0.4	0.2	0.4	<i>p</i> = 0.5 <i>q</i> = 0.5	0.6	0.5
Combined	<i>H_i</i> = 0.35			<i>p</i> = 0.5 <i>q</i> = 0.5	<i>H_S</i> = 0.5 <i>H_T</i> = 0.5	
<i>F_{ST}</i> = 0 <i>F_{IS}</i> = 0.3 <i>F_{IT}</i> = 0.3						
(B) Random mating populations with different allele frequencies						
1	0.25	0.5	0.25	<i>p</i> = 0.5 <i>q</i> = 0.5	0	0.5
2	0.04	0.32	0.64	<i>p</i> = 0.2 <i>q</i> = 0.8	0	0.32
Combined	<i>H_i</i> = 0.41			<i>p</i> = 0.35 <i>q</i> = 0.65	<i>H_S</i> = 0.41 <i>H_T</i> = 0.455	
<i>F_{ST}</i> = 0.099 <i>F_{IS}</i> = 0 <i>F_{IT}</i> = 0.099						
(C) Populations with different allele frequencies, one random mating, other inbreeding						
1	0.25	0.5	0.25	<i>p</i> = 0.5 <i>q</i> = 0.5	0	0.5
2	0.14	0.13	0.74	<i>p</i> = 0.2 <i>q</i> = 0.8	0.6	0.32
Combined	<i>H_i</i> = 0.31			<i>p</i> = 0.35 <i>q</i> = 0.65	<i>H_S</i> = 0.41 <i>H_T</i> = 0.455	
<i>F_{ST}</i> = 0.042 <i>F_{IS}</i> = 0.31 <i>F_{IT}</i> = 0.312						



Pacific yew

Example 14.4

Computation of F statistics for the rare Pacific yew

Average observed heterozygosity (H_I) for 21 allozyme loci across nine Canadian populations was 0.085, while the average expected heterozygosity for these populations (H_S) was 0.166 (El-Kassaby & Yanchuk 1994). Consequently, inbreeding within populations F_{IS} is

$$F_{IS} = 1 - \frac{H_I}{H_S} = 1 - \frac{0.085}{0.166} = 0.49$$

This high level of inbreeding is not due to selfing as the species is dioecious, but is probably due to offspring establishing close to parents and clumping of relatives from bird and rodent seed caches. The expected heterozygosity for the total nine populations (H_T) was 0.18. Thus inbreeding due to population differentiation (F_{ST}) is

$$F_{ST} = 1 - \frac{H_S}{H_T} = 1 - \frac{0.166}{0.180} = 0.078$$

This indicates only a modest degree of population differentiation. The total inbreeding due to both inbreeding within populations and differentiation among them (F_{IT}) is

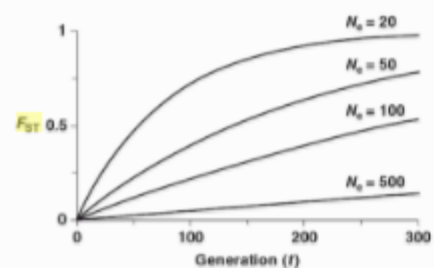
$$F_{IT} = 1 - \frac{H_I}{H_T} = 1 - \frac{0.085}{0.18} = 0.53$$

F_{ST} can be estimated using allozyme or microsatellite heterozygosity data. A related measure R_{ST} has also been devised for microsatellite data (Slatkin 1995), but comparative evaluations indicate little difference between this and F_{ST} for microsatellites (Balloux & Goudet 2002). A more serious issue is that F_{ST} does not scale 0–1 for markers with more than two alleles, such as microsatellites, and values are not comparable for different microsatellite loci and for allozymes versus microsatellites. To address this problem, Hedrick (2005c) has devised a standardized genetic differentiation measure, based upon scaling F_{ST} to its maximum value for the given data set.

Figure 14.8 illustrates more rapid increases in F_{ST} over generations in smaller populations than in larger ones. Typically, an F_{ST} above

F_{ST} increases over generations in fragmented populations at a rate inversely dependent on population size

Fig. 14.8 Theoretical increase in F_{ST} with generations in isolated fragments with different population sizes.



In real (non-idealized) populations, more than one migrant per generation is required to prevent fixation in population fragments

More than one migrant per generation is typically required in real populations, as migrants and residents are unlikely to be equally successful in producing offspring, and real populations do not exhibit idealized structures. Numbers of 5, 1–10 and >10 migrants per generation have been proposed (Lacy 1987; Mills & Allendorf 1996; Vucetich & Waite 2000). The complications arising from non-idealized structures are largely overcome by assessing N_m values where a value of 1 has the effect originally envisaged by Wright (Wang 2004a).

Inbreeding is reduced by migration among population fragments

Migration and inbreeding

Inbreeding can be substantially reduced by the introduction of individuals from other fragments (Chapter 13). This occurs even when the immigrants are themselves inbred, as long as they come from genetically distinct populations.

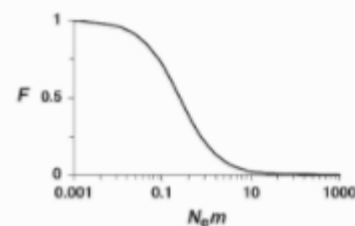
Inbreeding in population fragments depends on the effective population size and the migration rate

When population sizes and migration rates are constant, inbreeding and migration reach an equilibrium where the reduction in divergence due to migration balances the increase due to drift. This equilibrium, measured using F_{ST} , is (Wright 1969):

$$F_{\text{sr}} = \frac{1}{4 N_{\text{cm}} + 1} \quad (14.7)$$

This equation applies when m is small and all population sizes and migration rates among them are the same. Figure 14.10 illustrates the relationship between the number of migrants per generation ($N_e m$) and the inbreeding coefficient. With one migrant per generation, $F_{ST} = 1/(4 + 1) = 0.2$. Conversely, the inbreeding coefficient rises rapidly with less than one migrant per generation, and reaches 1.0 (complete divergence – fixation in populations) when there is no migration.

Fig. 14.10 Relationship between equilibrium inbreeding coefficient and the number of migrants per generation (N_m) for an island model at equilibrium between drift and migration.



Experimental studies support the expectations above (Bryant *et al.* 1999; Newman & Tallmon 2001). For example, populations of the canola plant maintained at sizes of five individuals per generation

