

# Lecture 5: Resemblance Between Relatives

Bruce Walsh lecture notes  
Tucson Winter Institute  
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# Heritability

- Central concept in quantitative genetics
- Fraction of phenotypic variance due to additive genetic values (Breeding values)
  - $h^2 = V_A/V_P$
  - This is called the **narrow-sense heritability**
  - Phenotypes (and hence  $V_P$ ) can be directly measured
  - Breeding values (and hence  $V_A$ ) must be estimated
- Estimates of  $V_A$  require **known collections of relatives**

# Broad-sense heritability

- Narrow-sense heritability  $h^2$  applies when outcrossing,
  - $h^2 = \text{Var}(A)/\text{Var}(P)$
  - = the fraction of all trait variation due to variation in breeding (additive genetic) values
- **Broad-sense heritability  $H^2$**  applies when selecting among a series of pure lines
  - $H^2 = \text{Var}(G)/\text{Var}(P)$
  - = the fraction of all trait variation due to variation in **Genotypic values**

# Defining $H^2$ for Plant Populations

Plant breeders often do not measure individual plants (especially with pure lines), but instead measure a **plot** or a **block** of individuals.

This replication can result in inconsistent measures of  $H^2$  even for otherwise identical populations.

Let  $z_{ijkl}$  denote the value of the  $l$ -th replicate in plot  $k$  of genotype  $i$  in environment  $j$ . We can decompose this value as

$$z_{ijkl} = G_i + E_j + GE_{ij} + p_{ijk} + e_{ijkl}$$

Effect of the  $k$ -th plot

deviations of individual plants within this plot

Suppose we replicate the genotype over  $e$  environments, with  $r$  plots (replicates) per environment, and  $n$  individuals per plot.

If we set our unit of measurement as the average over all plots, the phenotypic variance for the mean of line  $i$  becomes

$$\sigma^2(z_i) = \sigma_G^2 + \sigma_E^2 + \frac{\sigma_{GE}^2}{e} + \frac{\sigma_p^2}{er} + \frac{\sigma_e^2}{ern}$$

Thus,  $V_p$ , and  $H^2 = V_G/V_p$ , depend on our choice of  $e$ ,  $r$ , and  $n$

In order to compare broad-sense heritabilities we need to use a consistent design (same values of  $e$ ,  $r$ , and  $n$ )

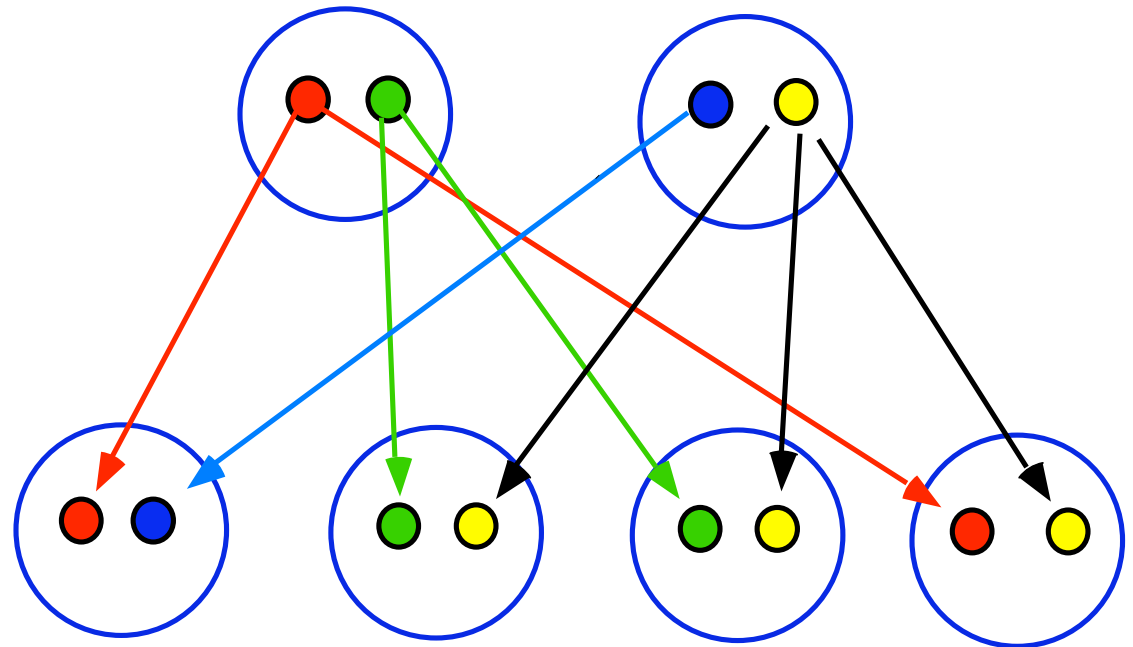
# Key observations

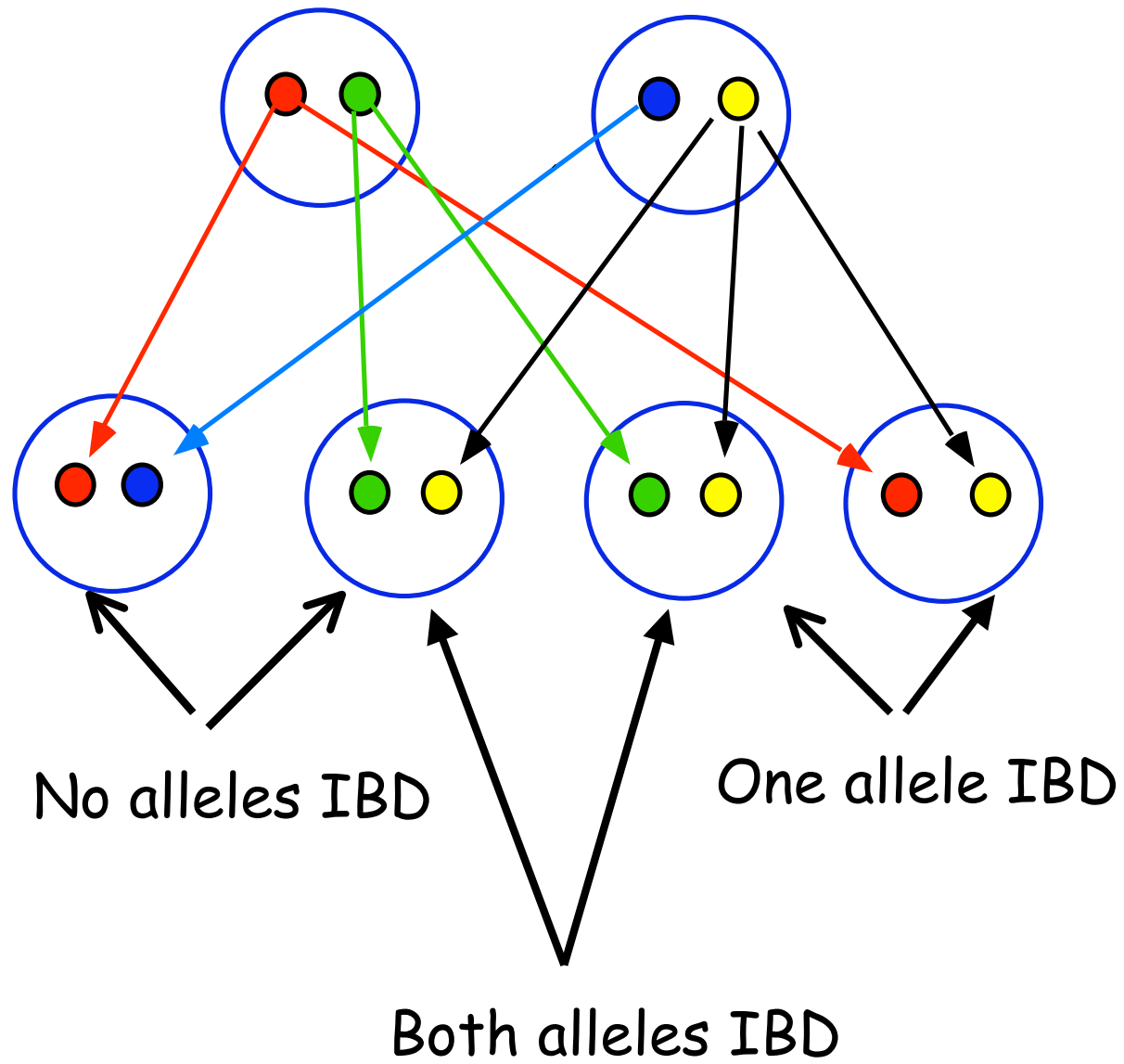
- The amount of **phenotypic resemblance** among relatives for the trait provides an indication of the amount of **genetic variation** for the trait.
- If trait variation has a significant genetic basis, the **closer the relatives**, the **more similar their appearance**
- The covariance between the phenotypic value of relatives measures the strength of this similarity, with larger Cov = more similarity

# Genetic Covariance between relatives

Sharing alleles means having alleles that are **identical by descent (IBD)**: both copies can be traced back to a single copy in a recent common ancestor.

Genetic covariances arise because two **related individuals are more likely to share alleles** than are two unrelated individuals.



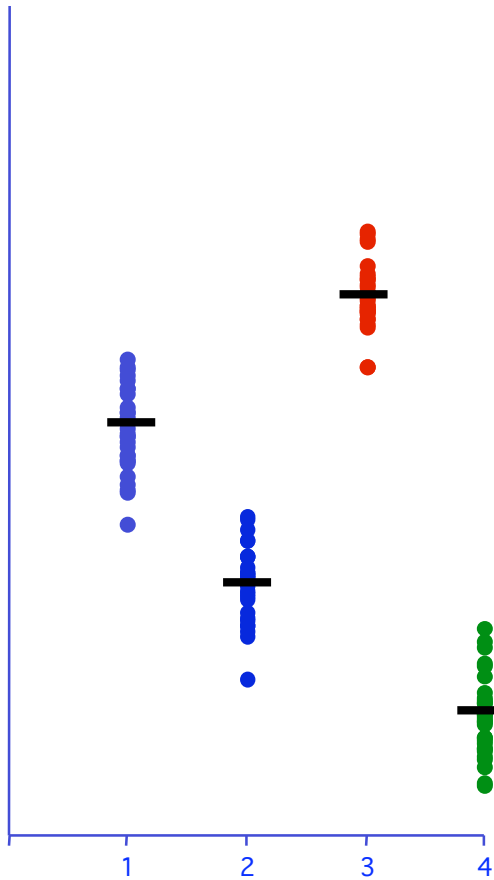




# ANOVA: Analysis of variation

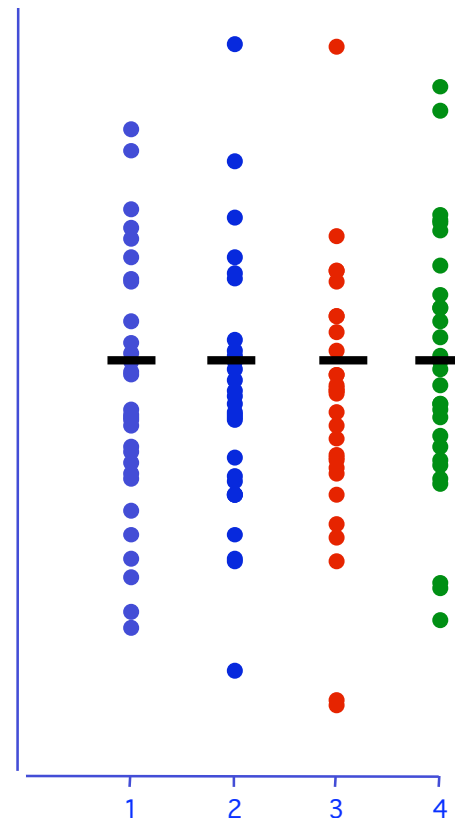
- Partitioning of trait variance into within- and among-group components
- Two key ANOVA identities
  - Total variance = between-group variance + within-group variance
    - $\text{Var}(T) = \text{Var}(B) + \text{Var}(W)$
  - Variance(between groups) = covariance (within groups)
  - Intraclass correlation,  $t = \text{Var}(B)/\text{Var}(T)$
- The more similar individuals are within a group (higher within-group covariance), the larger their between-group differences (variance in the group means)

### Situation 1



$$\begin{aligned} \text{Var}(B) &= 2.5 \\ \text{Var}(W) &= 0.2 \quad \dagger = 2.5/2.7 = 0.93 \\ \text{Var}(T) &= 2.7 \end{aligned}$$

### Situation 2



$$\begin{aligned} \text{Var}(B) &= 0 \\ \text{Var}(W) &= 2.7 \quad \dagger = 0 \\ \text{Var}(T) &= 2.7 \end{aligned}$$

# Why $\text{cov}(\text{within}) = \text{variance}(\text{among})$ ?

- Let  $z_{ij}$  denote the  $j$ th member of group  $i$ .
  - Here  $z_{ij} = u + g_i + e_{ij}$
  - $g_i$  is the group effect
  - $e_{ij}$  the residual error
- Covariance within a group  $\text{Cov}(z_{ij}, z_{ik})$ 
  - $= \text{Cov}(u + g_i + e_{ij}, u + g_i + e_{ik})$
  - $= \text{Cov}(g_i, g_i)$  as all other terms are uncorrelated
  - $\text{Cov}(g_i, g_i) = \text{Var}(g)$  is the among-group variance

# Resemblance between relatives and variance components

- The phenotypic variance between relatives can be expressed in terms of genetic variance components
  - $\text{Cov}(z_x, z_y) = a_{xy}V_A + b_{xy}V_D$ .
  - The weights  $a$  and  $b$  depend on the nature of the relatives  $x$  and  $y$ , and are measures of how often they are expected to share alleles identical by descent
  - These are critical in predicting selection response

# Parent-offspring genetic covariance

$\text{Cov}(G_p, G_o)$  --- Parents and offspring share  
**EXACTLY one allele IBD**

Denote this common allele by  $A_1$

$$G_p = A_p + D_p = \alpha_1 + \alpha_x + D_{1x}$$
$$G_o = A_o + D_o = \alpha_1 + \alpha_y + D_{1y}$$

IBD allele

Non-IBD alleles

$$\begin{aligned}
Cov(G_o, G_p) &= Cov(\alpha_1 + \alpha_x + D_{1x}, \alpha_1 + \alpha_y + D_{1y}) \\
&= Cov(\alpha_1, \alpha_1) + \cancel{Cov(\alpha_1, \alpha_y)} + \cancel{Cov(\alpha_1, D_{1y})} \\
&\quad + \cancel{Cov(\alpha_x, \alpha_1)} + \cancel{Cov(\alpha_x, \alpha_y)} + \cancel{Cov(\alpha_x, D_{1y})} \\
&\quad + \cancel{Cov(D_{1x}, \alpha_1)} + \cancel{Cov(D_{1x}, \alpha_y)} + \cancel{Cov(D_{1x}, D_{1y})}
\end{aligned}$$

All blue covariance terms are zero.

- By construction,  $\alpha$  and  $D$  are uncorrelated
- By construction,  $\alpha$  from non-IBD alleles are uncorrelated
- By construction,  $D$  values are uncorrelated unless both alleles are IBD

$$Cov(\alpha_x, \alpha_y) = \begin{cases} 0 & \text{if } x \neq y, \text{ i.e., not IBD} \\ Var(A)/2 & \text{if } x = y, \text{ i.e., IBD} \end{cases}$$

$$Var(A) = Var(\alpha_1 + \alpha_2) = 2Var(\alpha_1)$$

so that

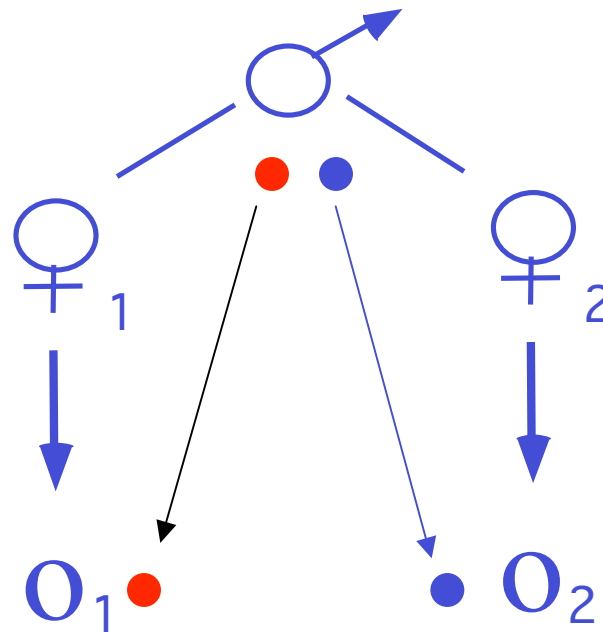
$$Var(\alpha_1) = Cov(\alpha_1, \alpha_1) = Var(A)/2$$

Hence, relatives sharing one allele IBD have a genetic covariance of  $Var(A)/2$

The resulting parent-offspring genetic covariance becomes  $Cov(G_p, G_o) = Var(A)/2$

# Half-sibs

Each sib gets exactly one allele from common father, different alleles from the different mothers

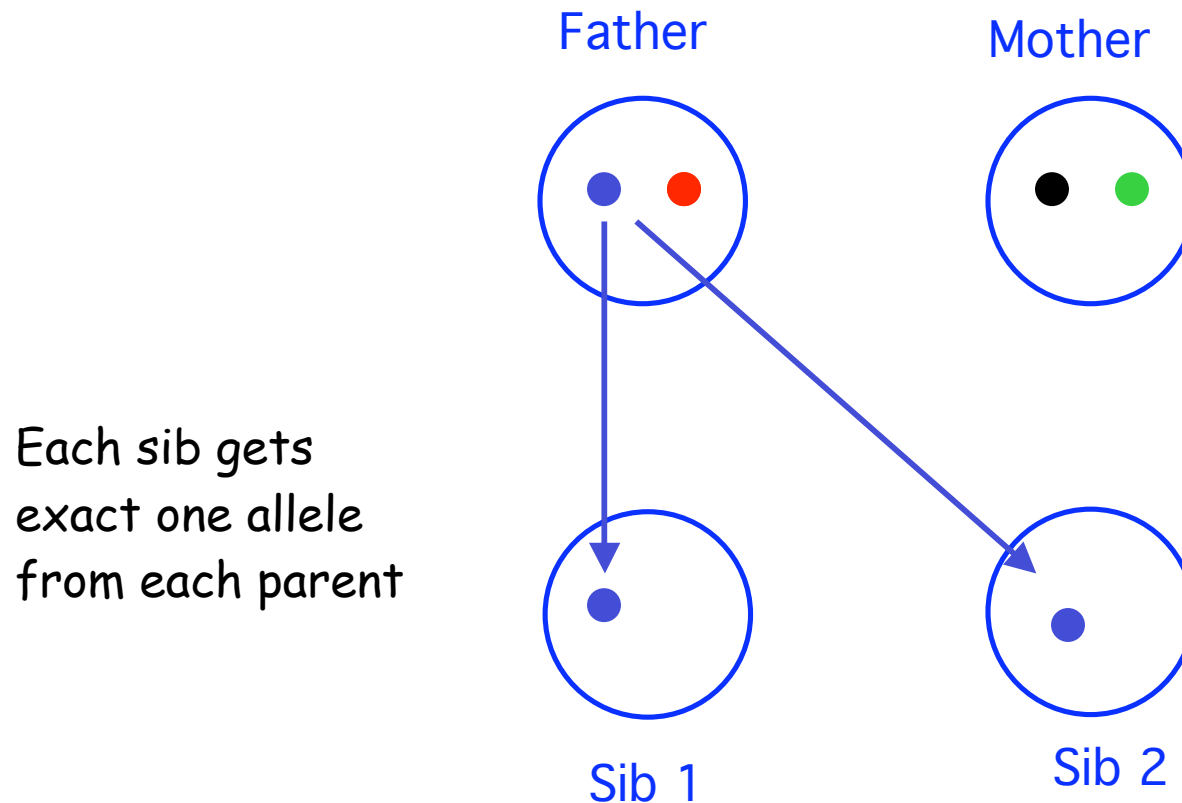


The half-sibs share no alleles IBD  
• occurs with probability 1/2

Hence, the genetic covariance of half-sibs is just  
 $(1/2)\text{Var}(A)/2 = \text{Var}(A)/4$



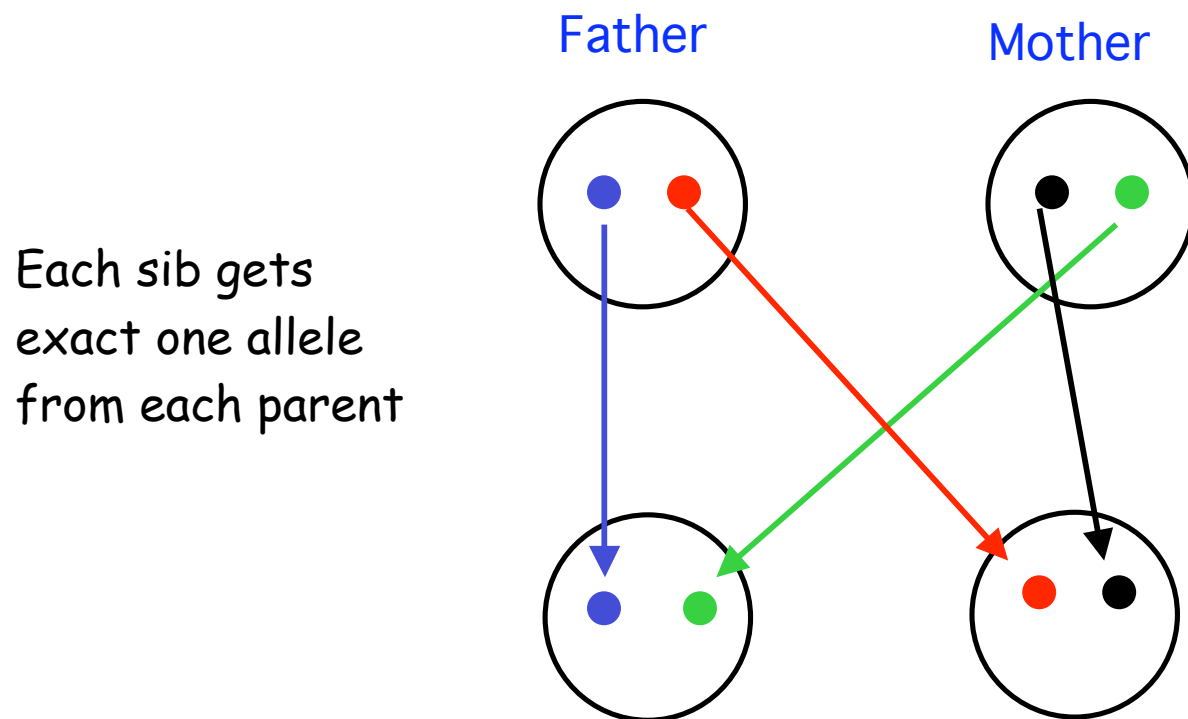
# Full-sibs



$\text{Prob}(\text{Allele from father IBD}) = 1/2$ . Given the allele in parent one, prob =  $1/2$  that sib 2 gets same allele

$\text{Prob}(\text{Allele from father not IBD}) = 1/2$ . Given the allele in parent one, prob =  $1/2$  that sib 2 gets different allele

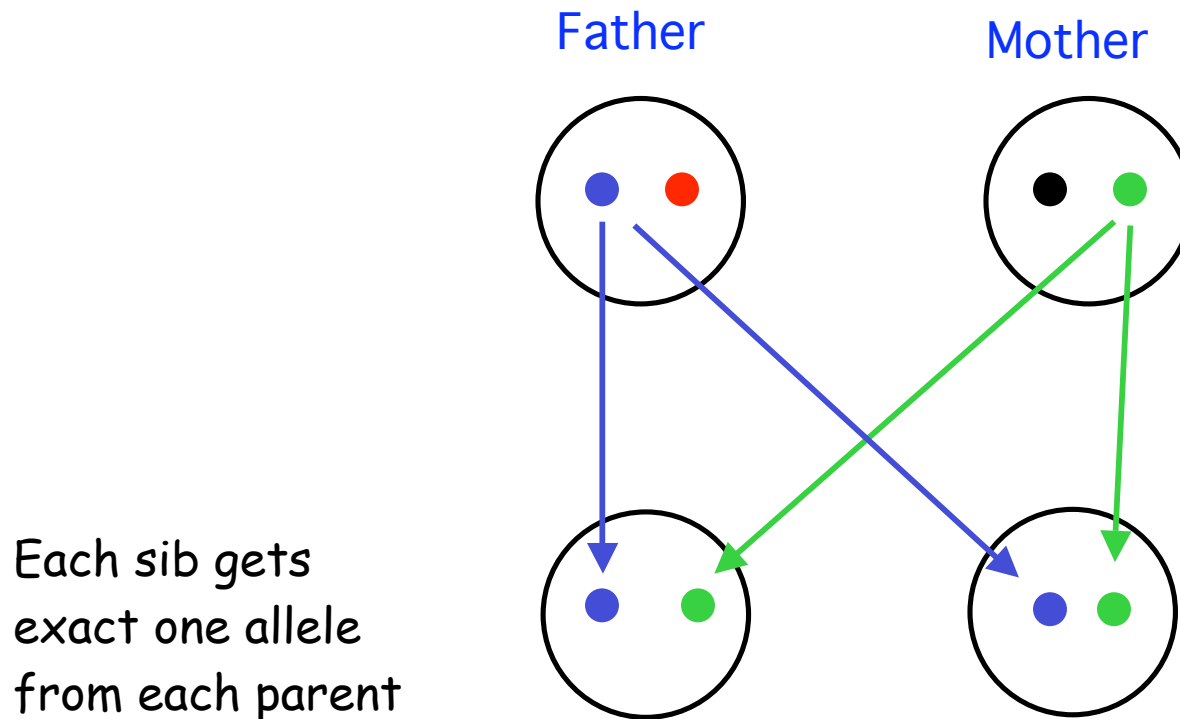
# Full-sibs



Paternal allele not IBD [ Prob =  $1/2$  ]

Maternal allele not IBD [ Prob =  $1/2$  ]

Prob(sibs share 0 alleles IBD) =  $1/2 * 1/2 = 1/4$



Paternal allele IBD [ Prob = 1/2 ]

Maternal allele IBD [ Prob = 1/2 ]

Prob(sibs share 2 alleles IBD) =  $1/2 * 1/2 = 1/4$

Prob(share 1 allele IBD) =  $1 - \text{Pr}(0) - \text{Pr}(2) = 1/2$

## Resulting Genetic Covariance between full-sibs

IBD alleles	Probability	Contribution
0	1/4	0
1	1/2	$\text{Var}(A)/2$
2	1/4	$\text{Var}(A) + \text{Var}(D)$

---

$$\text{Cov}(\text{Full-sibs}) = \text{Var}(A)/2 + \text{Var}(D)/4$$

# Genetic Covariances for General Relatives

Let  $r = (1/2)\text{Prob}(1 \text{ allele IBD}) + \text{Prob}(2 \text{ alleles IBD})$

Let  $u = \text{Prob}(\text{both alleles IBD})$

General genetic covariance between relatives

$$\text{Cov}(G) = r\text{Var}(A) + u\text{Var}(D)$$

When epistasis is present, additional terms appear

$$r^2\text{Var}(AA) + ru\text{Var}(AD) + u^2\text{Var}(DD) + r^3\text{Var}(AAA) +$$

# More general relationships

- To obtain the expected covariance for any set of relatives, we normally need only compute  $r$  and  $u$  for that set of relatives
- With general inbreeding, becomes more complex (as three other terms, in addition to  $V_A$  and  $V_D$  arise --- not discussed here, see WL chapter 5 for details)
- With crosses involving inbred and/or related parents, values for  $r$  and  $u$  are different from those presented above.

# Coefficients of Coancestry

Suppose we pick a single allele each at random from two relatives. The probability that these are IBD is called  $\Theta$ , the **coefficient of coancestry**

$\Theta_{xy}$  denotes the coefficient for relatives  $x$  and  $y$

Consider an offspring  $z$  from a (hypothetical) cross of  $x$  and  $y$ .  $\Theta_{xy} = f_z$ , the inbreeding coefficient of  $z$ . Why? Because the offspring of  $x$  and  $y$  each get a randomly-chosen allele from each parent. The probability  $f_z$  that both alleles are IBD (the probability of inbreeding) is thus just  $\Theta_{xy}$ .

# $\theta$ and the coefficient on $V_A$

- The coefficient on the additive variance for the relatives  $x$  and  $y$  is just  $2\theta_{xy}$ .
- To see this,
  - let  $A_i A_j$  denote the two alleles in  $x$  and  $A_k A_l$  those in  $y$ .
  - $\text{Cov}(\text{breeding values}) = \Pr(A_i \text{ ibd } A_k) \text{cov}(\alpha_i, \alpha_k) + \Pr(A_i \text{ ibd } A_l) \text{cov}(\alpha_i, \alpha_l) + \Pr(A_j \text{ ibd } A_k) \text{cov}(\alpha_j, \alpha_k) + \Pr(A_j \text{ ibd } A_l) \text{cov}(\alpha_j, \alpha_l) = 4 \theta_{xy} \text{Var}(\alpha)$
  - Since  $\text{Var}(A) = 2\text{Var}(\alpha)$ ,  $\text{Cov} = 2 \theta_{xy} \text{Var}(A)$



# $\Theta_{xx}$ : The Coancestry of an individual with itself

Self  $x$ , what is the inbreeding coefficient of its offspring?

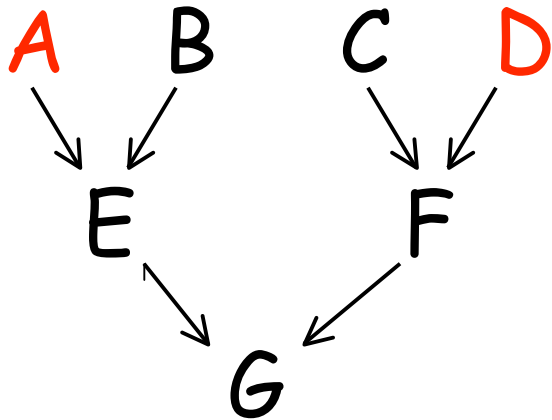
To compute  $\Theta_{xx}$ , denote the two alleles in  $x$  by  $A_1$  and  $A_2$

	Draw $A_1$	Draw $A_2$
Draw $A_1$	IBD	$f_x$
Draw $A_2$	$f_x$	IBD

Hence, for a non-inbred individual,  $\Theta_{xx} = 2/4 = 1/2$

If  $x$  is inbred,  $f_x = \text{prob } A_1 \text{ and } A_2 \text{ IBD}$ ,  $\Theta_{xx} = (1 + f_x)/2$

# Example

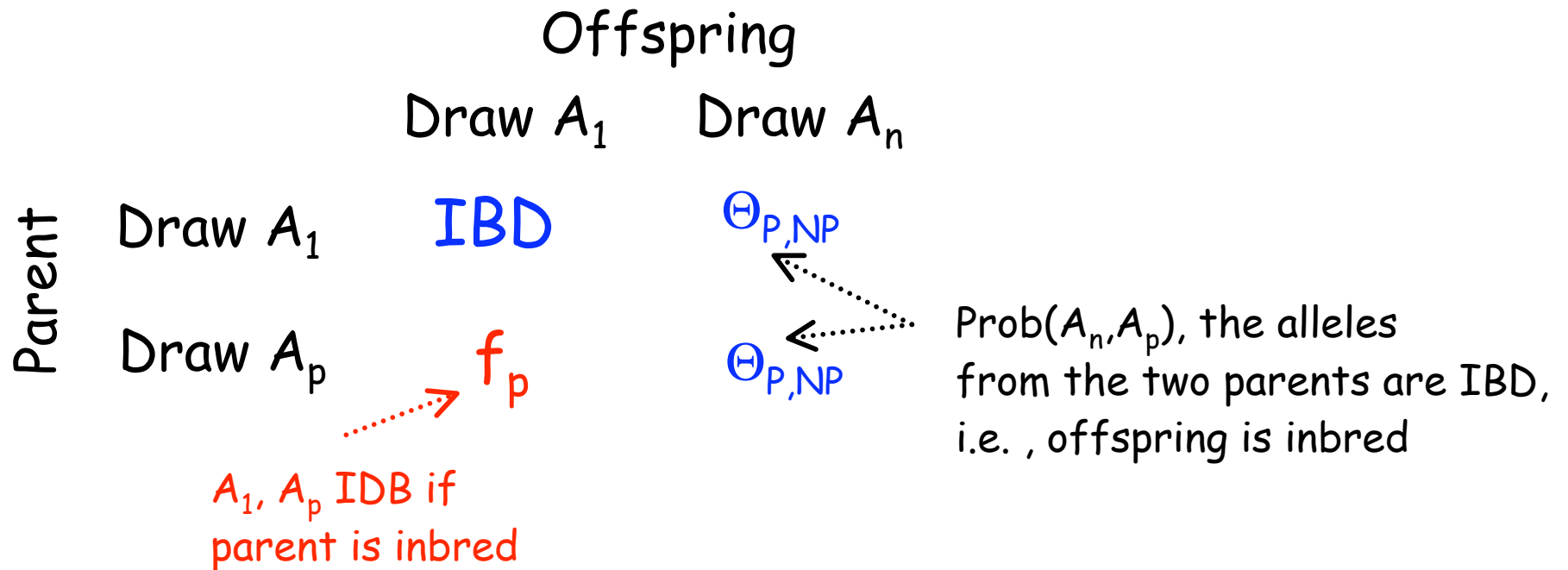


Consider the following pedigree  
Suppose **A** and **D** are **fully-inbred**,  
and related, lines with  $\theta_{AD} = 0.5$ .  
Further, B and C are unrelated and  
outcrossed individuals

Individual	A	B	C	D
$F_x$	1	0	0	1
$\theta_{xx} = (1 + F_x)/2$	1	1/2	1/2	1

# The Parent-offspring Coancestry

Let  $A_1, A_n$  denote the two alleles in the offspring, where  $A_n$  is the allele from the nonfocal parent (NP), while  $A_1, A_p$  are the two alleles in the focal parent (P)



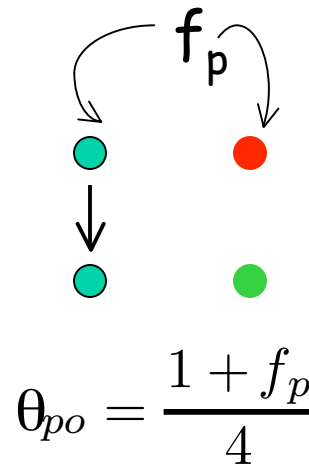
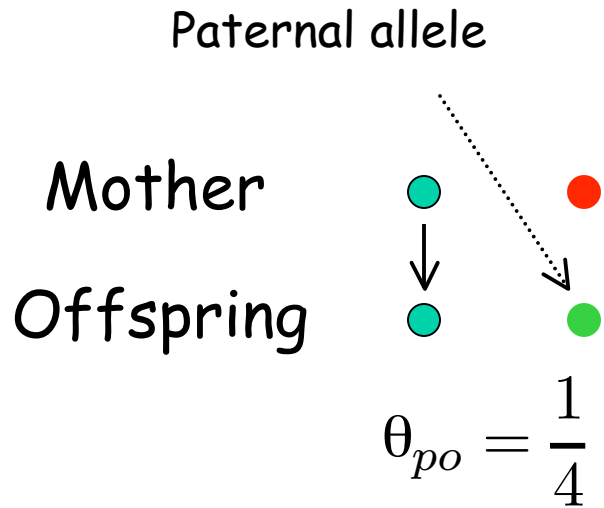
For a non-inbred individual,  $\Theta_{PO} = 1/4$

General:

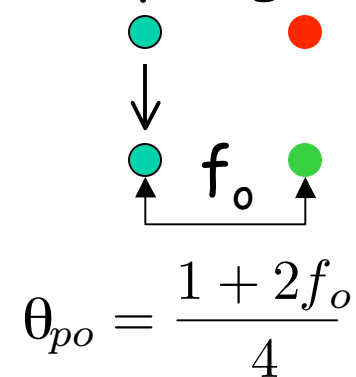
$$\Theta_{PO} = (1 + f_p + 2\Theta_{P,NP})/4 = (1 + f_p + 2f_o)/4$$

# $\Theta_{op}$ = Parent & Offspring

Parent inbred



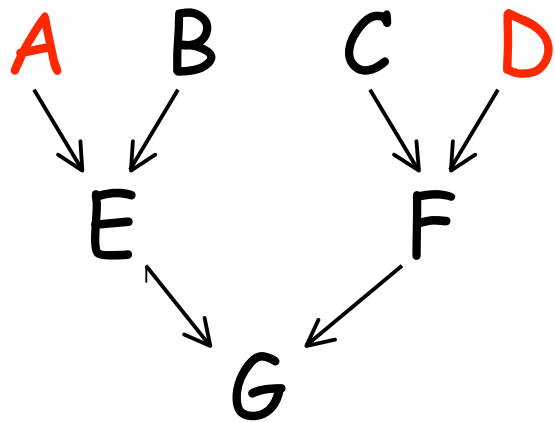
Offspring inbred



$1/2$  = Prob random offspring allele from father. Prob =  $\theta_{mf} = f_o$  that this allele is IBD to mother giving a contribution of  $f_o/2$

$$\theta_{po} = \frac{1}{4}(1 + f_p + 2\theta_{mf})$$

This is just  $2f_o$



From before

$$\theta_{AA} = \theta_{DD} = 1; \theta_{BB} = \theta_{CC} = 1/2;$$

$$\theta_{AD} = 1/2,$$

$$\theta_{AB} = \theta_{AC} = \theta_{BC} = \theta_{BD} = \theta_{CD} = 0$$

Consider A - E (inbred parent - offspring)

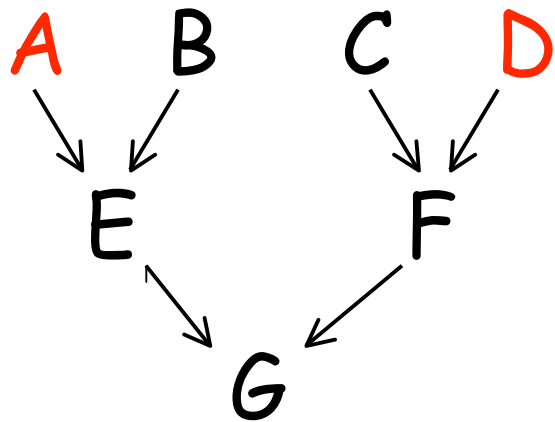
$$\theta_{AE} = (1+f_A)/4 = (1+1)/4 = 1/2. \text{ Same value for } \theta_{DF}$$

Consider B - E (outbred parent - offspring)

$$\theta_{BE} = (1+f_B)/4 = (1+0)/4 = 1/4. \text{ Same value for } \theta_{CF}$$

Consider E - G (outbred parent - offspring)

$$\theta_{EG} = (1+f_E)/4 = (1+0)/4 = 1/4. \text{ Same value for } \theta_{FG}$$



From before

$$\theta_{AA} = \theta_{DD} = 1; \theta_{BB} = \theta_{CC} = 1/2;$$

$$\theta_{AD} = 1/2,$$

$$\theta_{AB} = \theta_{AC} = \theta_{BC} = \theta_{BD} = \theta_{CD} = 0$$

What about  $\theta_{EF}$ ?

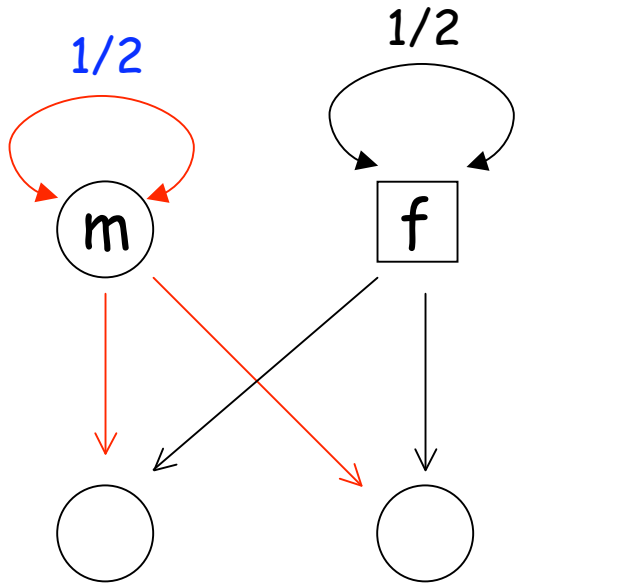
The randomly-chosen allele from E has equal chance of being from A or B. Likewise for F (from C or D)

Of these four possible combinations (A&C, A&D, B&C, B&D), only an allele from A and an allele from D have a chance of being IBD, which is  $\theta_{AD} = 1/2$ .

$$\text{Hence, } \theta_{EF} = \theta_{AD} / 4 = 1/8$$

# Full sibs (x and y) from parents m and f

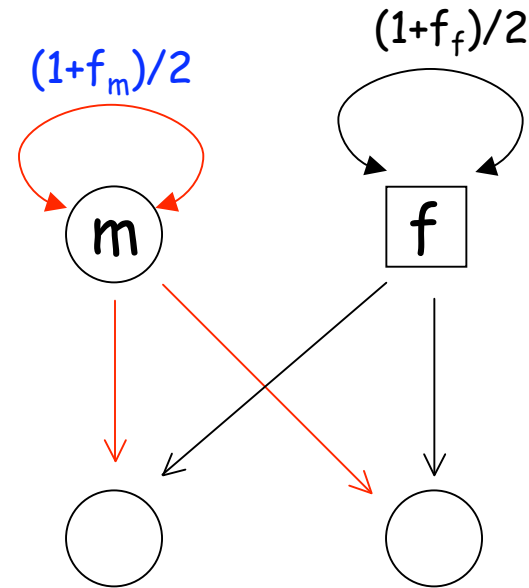
$$\Theta = 1/8 + 1/8 = 1/4$$



$$(1/2)(1/2)(1/2) \quad (1/2)(1/2)(1/2)$$

Unrelated, non-inbred  
parents

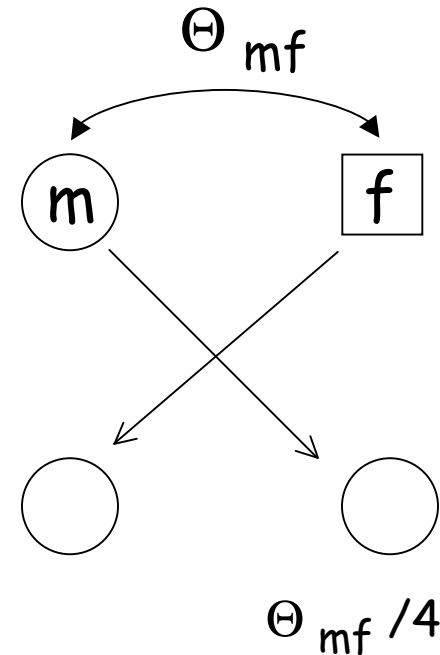
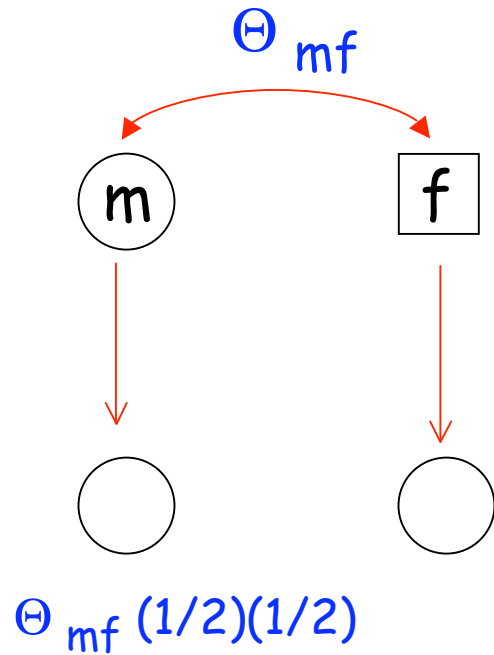
$$\Theta = (2 + f_m + f_f)/8$$



$$[(1 + f_m)/2] (1/2)(1/2) \quad [(1 + f_f)/2] (1/2)(1/2)$$

Unrelated, inbred  
parents

# Full sibs (x and y) from parents m and f



Parents inbred & related.

Two additional paths to add

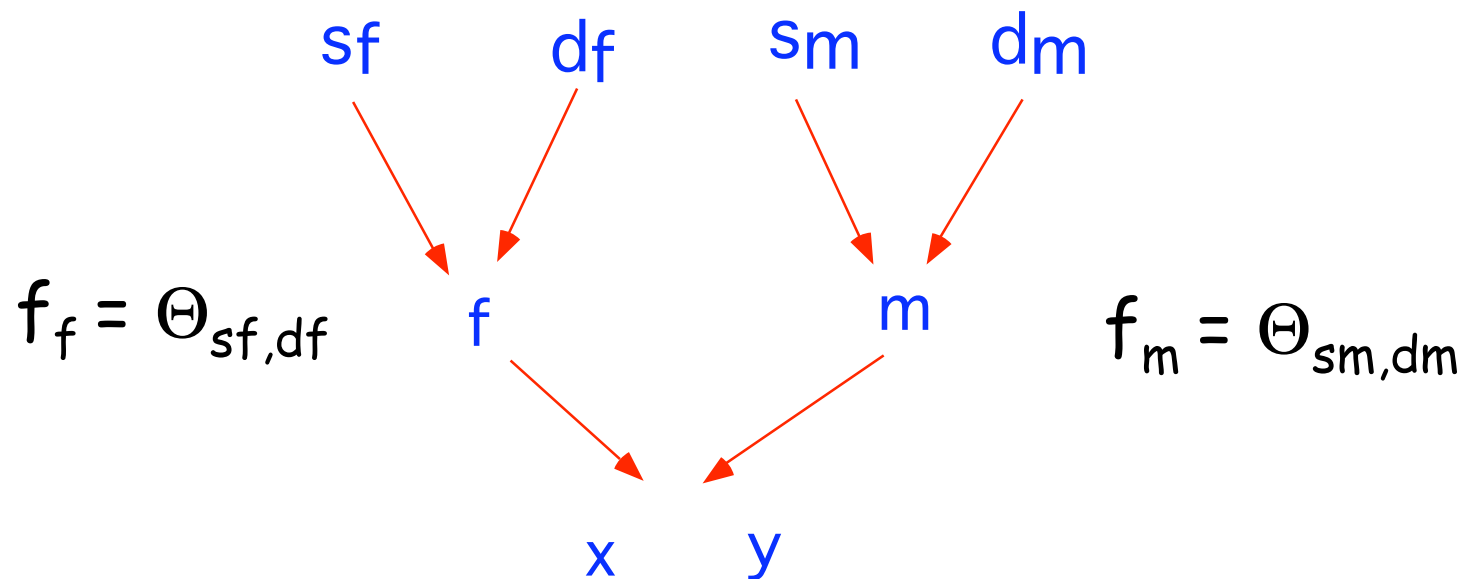
to  $\Theta = (2 + f_m + f_f) / 8$

This gives  $\Theta = (2 + f_m + f_f + 4 \Theta_{mf}) / 8$



Full sibs (x and y) from parents m and f

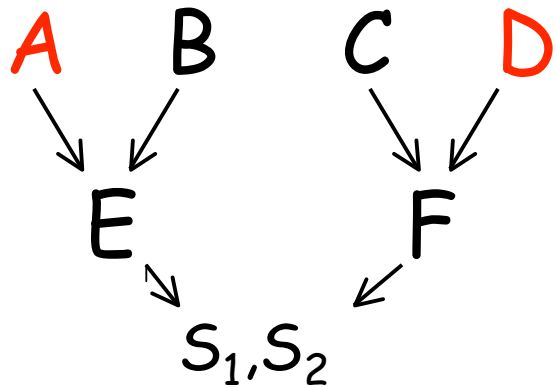
$$\Theta_{xy} = (2 + f_m + f_f + 4\Theta_{mf})/8$$



Putting all this together gives

$$\Theta_{xy} = (2 + \Theta_{sm,dm} + \Theta_{sf,df} + 4\Theta_{mf})/8$$

# Example



From before

$$\theta_{AA} = \theta_{DD} = 1; \theta_{BB} = \theta_{CC} = 1/2;$$

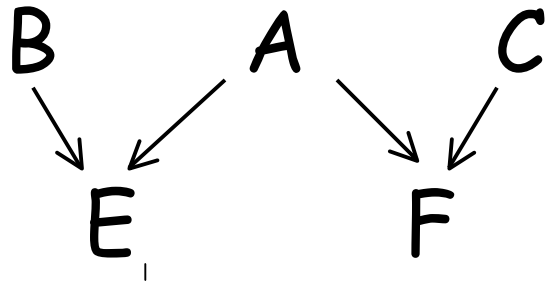
$$\theta_{AD} = 1/2, \theta_{EF} = 1/8,$$

$$\theta_{AB} = \theta_{AC} = \theta_{BC} = \theta_{BD} = \theta_{CD} = 0$$

$$\Theta_{xy} = (2 + \Theta_{AB} + \Theta_{CD} + 4\Theta_{EF})/8$$

$$\theta_{S_1 S_2} = (2 + 0 + 0 + 4[1/8])/8 = (4 + 1)/16 = 5/16$$

# Half-sibs



A is the common parent

- Using the same arguments as above,

$$\begin{aligned}\theta_{EF} &= (\theta_{AA} + \theta_{AB} + \theta_{AC} + \theta_{BC})/4 \\ &= ([1 + f_A]/2 + \theta_{AB} + \theta_{AC} + \theta_{BC})/4\end{aligned}$$

Hence, if B and C unrelated,

$$\theta_{EF} = (1 + f_A)/8$$

# Computing $\Theta_{xy}$ -- chain counting

$\Theta$  can be obtained for any structure of pedigree

Two components: First are paths through a single common ancestor (i) of both x and y

$$\Theta_{xy} = \sum_i \Theta_{ii} \binom{1}{2}^{n_i-1} + \sum_j \sum_{j=k} \Theta_{jk} \binom{1}{2}^{n_{jk}-2}$$

Coefficient of coancestry of i

$n_i$  = Number of individuals (including x and y) in path connecting x and y through i

# Computing $\Theta_{xy}$ -- chain counting

Second component: Paths from x through j and paths from y through k, j & k related

$$\Theta_{xy} = \sum_i \Theta_{ii} \binom{1}{2}^{n_i-1} + \sum_j \sum_{j=k} \Theta_{jk} \binom{1}{2}^{n_{jk}-2}$$

Coefficient of coancestry  
of j and k

Number of individuals,  
including x and y  
on the path leading  
from two different  
(but related) ancestors  
j and k

# The coefficient of fraternity

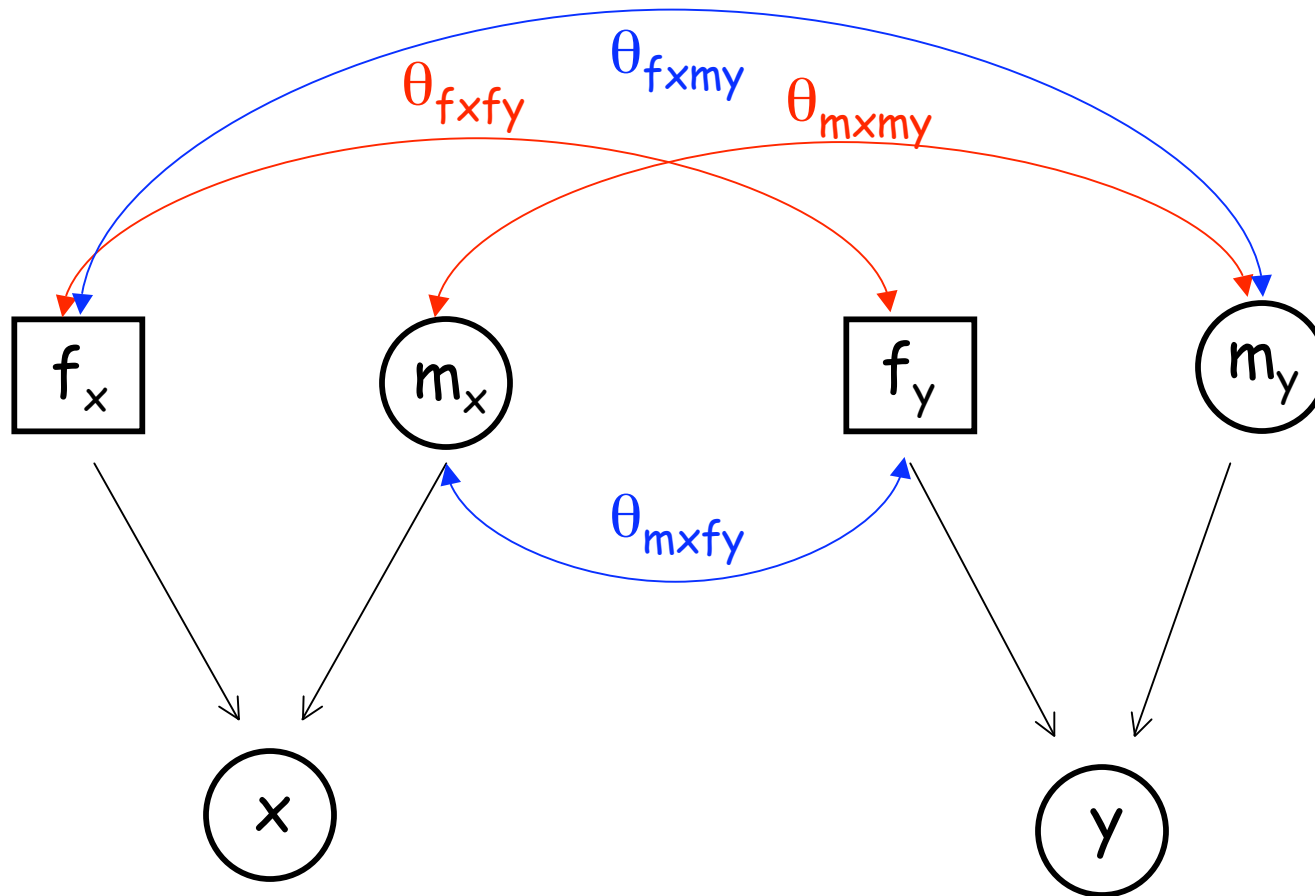
- While (twice) the coefficient of coancestry gives the weight on the additive variance for two relatives, a related measure of IBD status among relatives gives the weight on the dominance variance
- The probability that the two alleles in individual  $x$  are IBD to two alleles in individual  $y$  is denoted  $\Delta_{xy}$ , and is called the **coefficient of fraternity**.
- This can be expressed as a function of the coefficients of coancestry for the parents of ( $m_x$  and  $f_x$ ) of  $x$  and the parents ( $m_y$  and  $f_y$ ) of  $y$ .
  - $\Delta_{xy} = \theta_{m_x m_y} \theta_{f_x f_y} + \theta_{m_x f_y} \theta_{f_x m_y}$

# The coefficient of fraternity (cont)

- x and y can have both alleles IBD if
  - The allele from the father (fx) of x and the father (fy) of y are IBD (probability  $\theta_{fxfy}$ ) AND the allele from the mother (mx) of x and the mother (my) of y are IBD (probability  $\theta_{mxmy}$ ) , or  $\theta_{fxfy} \theta_{mxmy}$
  - OR the allele from the mother (mx) of x and the father (fy) of y are IBD (probability  $\theta_{mxfy}$ ) AND the allele from the father (fx) of x and the mother (my) of y are IBD (probability  $\theta_{fxmy}$ ) , or  $\theta_{mxfy} \theta_{fxmy}$
  - Putting these together gives
    - $\Delta_{xy} = \theta_{mxmy} \theta_{fxfy} + \theta_{mxfy} \theta_{fxmy}$

# $\Delta_{xy}$ , The Coefficient of Fraternity

$\Delta_{xy} = \text{Prob}(\text{both alleles in } x \text{ \& } y \text{ IBD})$



$$\Delta_{xy} = \theta_{mxmy}\theta_{fxfy} + \theta_{mxfy}\theta_{fxmy}$$



# Examples of $\Delta_{xy}$ : Full sibs

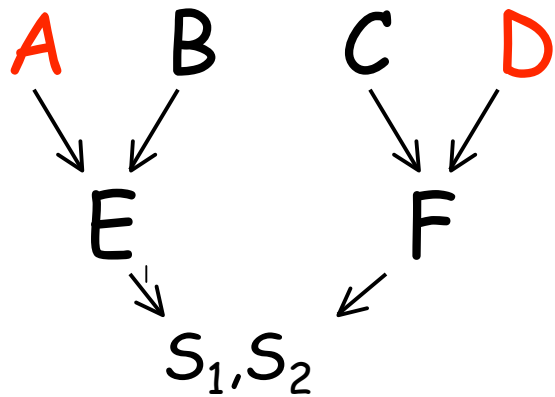
- Full sibs share same mon, dad
  - $m_x = m_y = m, f_x = f_y = f$
  - $\Delta_{xy} = \theta_{m \times m y} \theta_{f \times f y} + \theta_{m \times f y} \theta_{f \times m y} = \theta_{mm} \theta_{ff} + \theta_{mf}^2$
  - $\Delta_{xy} = (1+f_m)(1+f_f)/4 + \theta_{mf}^2$
- If parents unrelated,  $\theta_{fm} = 0$ , giving
  - $\Delta_{xy} = (1+f_m)(1+f_f)/4$
- If parents are unrelated and not inbred,
  - $\Delta_{xy} = 1/4$

# Examples of $\Delta_{xy}$ : Half sibs

- Paternal half sibs share same dad, different moms
  - $f_x = f_y = f$ ;  $m_x$  and  $m_y$
  - $\Delta_{xy} = \theta_{m_x m_y} \theta_{f_x f_y} + \theta_{m_x f_y} \theta_{f_x m_y} = \theta_{m_x m_y} \theta_{ff} + \theta_{m_x f} \theta_{m_y f}$
  - $\Delta_{xy} = \theta_{m_x m_y} (1+f_m)/2 + \theta_{m_x f} \theta_{m_y f}$
- If mothers are unrelated to each other and to the common father,  $\theta_{m_x m_y} = \theta_{m_x f} = \theta_{m_y f} = 0$ , giving
  - $\Delta_{xy} = 0$

# When is $\Delta$ non-zero?

- Since  $\Delta_{xy} = \theta_{mxmy}\theta_{fxfy} + \theta_{mxfy}\theta_{fxmy}$
- A nonzero value for  $\Delta$  requires either
  - That the fathers of both x and y are related AND the mothers of both x and y are related
  - OR that the father of x is related to the mother of y AND the mother of x is related to the father of y



From before

$$\theta_{AA} = \theta_{DD} = 1; \theta_{BB} = \theta_{CC} = 1/2;$$

$$\theta_{AD} = 1/2, \theta_{EF} = 1/8,$$

$$\theta_{AB} = \theta_{AC} = \theta_{BC} = \theta_{BD} = \theta_{CD} = 0$$

What is  $\Delta$  for the full sibs ( $S_1$  and  $S_2$ )?

$$\Delta_{xy} = \theta_{m \times m y} \theta_{f \times f y} + \theta_{m \times f y} \theta_{f \times m y} = \theta_{EE} \theta_{FF} + \theta_{EF}^2$$

$$\begin{aligned} \text{Giving } \Delta_{xy} &= \theta_{EE} \theta_{FF} + \theta_{EF}^2 \\ &= (1/2)(1/2) + (1/8)^2 \\ &= 1/4 + 1/64 = 17/64 = 0.266 \end{aligned}$$

# $\Delta_{xy}$ and the coefficient on $V_D$

- The coefficient on the dominance variance for the relatives  $x$  and  $y$  is just  $\Delta_{xy}$ .
- To see this,
  - let  $A_i A_j$  denote the two alleles in  $x$  and  $A_k A_l$  those in  $y$ .
  - Suppose that alleles  $i$  and  $k$  come from the mothers of these two relatives and alleles  $j$  and  $l$  from their fathers.
  - $\text{Cov}(\text{dominance values}) = \Pr(A_i \text{ ibd } A_k, A_j \text{ ibd } A_l) \text{cov}(\delta_{ij}, \delta_{kl}) + \Pr(A_i \text{ ibd } A_l, A_j \text{ ibd } A_k) \text{cov}(\delta_{ij}, \delta_{kl})$
  - $= (\theta_{fxfy} \theta_{mxmy} + \theta_{mxfy} \theta_{jxmy}) \text{Var}(D) = \Delta_{xy} \text{Var}(D)$

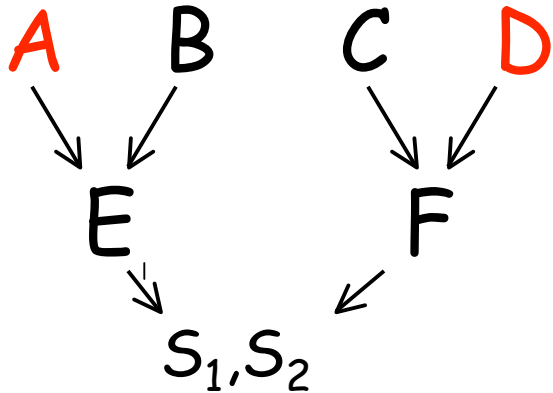
# General Resemblance between relatives

$$2\theta_{xy} = r_{xy}, \quad u_{xy} = \Delta_{xy}$$

$$\text{Cov}(G_x, G_y) = 2\theta_{xy}V_A + \Delta_{xy}V_D$$

$$\begin{aligned} \text{Cov}(G_x, G_y) &= 2\theta_{xy}V_A + \Delta_{xy}V_D \\ &\quad + (2\theta_{xy})^2V_{AA} + 2\theta_{xy}\Delta_{xy}V_{AD} + \Delta_{xy}^2V_{DD} + \dots \end{aligned}$$

# Example



We found for full sibs  $S_1, S_2$  that  $\theta = 5/16$ , hence  $2\theta = 5/8$ ;  $\Delta = 17/64$

Expected genetic covariance between this sibs is

$$(5/8)\text{Var}(A) + (17/64)\text{Var}(D) + (5/8)^2\text{Var}(AA) + (5/8)(17/64)\text{Var}(AD) + (17/64)^2\text{Var}(DD) + \dots$$

# Covariance among selfed lines

- A common situation in plant breeding is that two inbred lines are crossed
  - the frequency of any segregating allele in the  $F_1/F_2$  is 1/2
  - Starting with the  $F_1$ , a series of lines is formed by selfing,  $S_k = F_{2+k}$ .
  - The covariance among the various  $S_k$  lines is important in the response to selection in selfed lines
  - In particular, we want to covariance between an  $S_j$  and an  $S_k$  line whose last common ancestor was the  $S_i$ , with  $i \leq j \leq k$

$$\text{Cov}(S_j, S_k | S_i) = (1 + F_{S_i}) \left( V_A + \frac{(1 - F_{S_j})(1 - F_{S_k})}{1 - F_{S_i}} V_D \right)$$



# Autotetraploids

- Peanut, Potato, alfalfa, soybeans all examples of crops with at least some autotetraploid lines
- With autotetraploid, four alleles per locus, with a parent passing along two alleles to an offspring
- As a result, a parent can pass along the dominance contribution in  $G$  to an offspring
- Further, now there are four variance components associated with each locus

# Genetic variances for autotetraploids

- $G = A + D + T + Q$ 
  - A (additive) and D (dominance, or **digenic effects**) as with diploids
  - T (**trigenic effects**) are the three-way interactions among alleles at a locus
  - Q (**quadrigenic effects**) are the four-way interactions at a locus
- Total genetic variance becomes
  - $V_G = V_A + V_D + V_T + V_Q$

# Resemblance between autotetraploid relatives

Relatives	$V_A$	$V_D$	$V_T$	$V_Q$
Half-sibs	1/4	1/36		
Full-sibs	1/2	2/9	1/12	1/36
Parent-offspring	1/2	1/6		

Assumes unrelated, non-inbred parents