Kin value: relatedness, reproductive value & mating success

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Aims & Objectives

Aims

1. To show where regression relatedness, sex-specific reproductive value, and sex-specific mating success come from and how they affect the efficiency by which one organism can transmit another's genes.

2. To show how to combine these three parameters to determine the value of one organism to another (kin value) and so to determine the interests of different colony members over colony reproduction.

Objectives

1. To understand in general terms what regression relatedness, sex-specific reproductive value, and sex-specific mating success mean and where they come from.

2. To understand how to combine regression relatedness, sex-specific reproductive value, and sex-specific mating success to determine kin value.

Passing on Genes Indirectly

(In a Social Context)

Passing on Genes Indirectly

Workers can generally rear a range of individuals into reproductives:

males versus females (young queens)

brothers versus sons versus nephews

full sister queens versus half sister queens

Which of these should be reared?

In what ratio (sex ratio) should males and queens be reared?

Is there conflict? Among workers? Between workers and queen?

Should workers allow each other to produce males?

In general, natural selection will cause a worker to rear those individuals which are best at transmitting the worker's genes. These are the individuals with the greatest kin value. Kin value has three components

regression relatedness

sex-specific reproductive value

sex-specific mating success.

Conflicts & Conflict Resolution in Social Groups

How Did Eusociality Evolve?
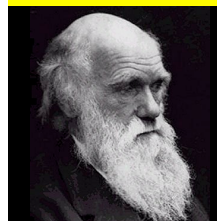
Charles Darwin (1859)

Not solved

William Hamilton 1964

Solved

Inclusive Fitness/Kin Selection

Workers help rear kin (e.g., brothers & sisters). Pass on genes indirectly.

Inclusive Fitness Theory

W. D. Hamilton

The Genetical Evolution of Social Behaviour

Journal of Theoretical Biology. 1964. 7: I-52

"Inclusive Fitness Theory"

(also known as "Kin Selection")

"The social behaviour of a species evolves in such a way that in each distinct behaviour-evoking situation the individual will seem to value his neighbours' fitness against his own according to the coefficients of relationship appropriate to that situation."

Relatedness Among Nestmates
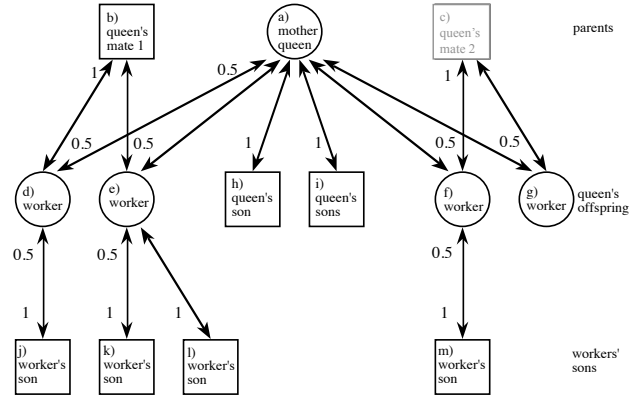
Determining genetic relatedness by probabilities of gene transmission

Queen Honey Bee Laying Egg

Most males are the queen's sons. Why are few workers' sons reared?

Worker Policing in Honey Bee

Worker policing: workers may prevent each other from reproducing by killing worker-laid eggs. Worker policing was predicted from IF theory.

Worker Policing in Saxon Wasp

Worker policing occurs in many species, like *Dolichovespula saxonica* the Saxon wasp. It is an important conflict resolution mechanism.

Crime Detection & Prevention

Policing in humans both detects and prevents crime. Crime prevention is probably more important than detection in reducing the harm done to society by criminal actions, and was the philosophy behind setting up the London force in the early 19th century. In insect societies, worker policing acts in both ways. By killing worker-laid eggs, police workers "detect" and "solve" antisocial acts. But in societies with effective egg policing few workers (honey bee, <0.1%) even try to lay eggs.

Regression Relatedness

Regression Relatedness to Self or Clonemate
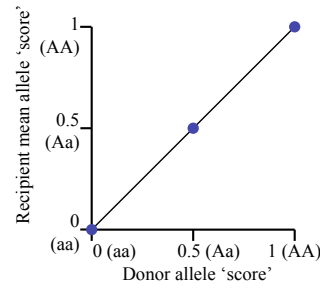
Here we compare the genotype of one individual (donor) with the genotype of another individual (recipient) at a single locus. The genotypes are converted into numbers by giving a score depending on how much of the genotype is allele A. Thus, aa scores 0, Aa scores 0.5, & AA 1.

There is a perfect correlation between the scores of the two individuals, as they always have the same genotype. If donor is aa so is recipient; if donor is AA so is recipient.

The gradient of the regression through these points is 1.

The regression relatedness is 1.

Regression Relatedness to Random Individual

Freq. of allele A in population
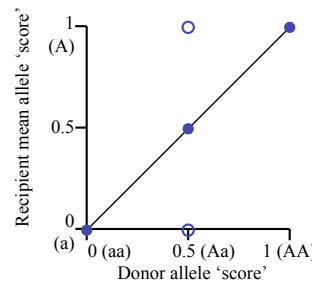- - - ● - - - 0.25   —●— 0.67
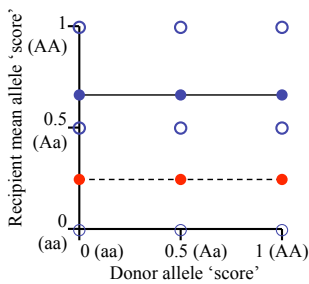
Here we compare the genotype of a donor individual with the genotypes of randomly chosen individuals in the same population.

The gradient of the regression of the gene scores is zero meaning that there is no correlation between the scores of the donor and the recipients.

The regression relatedness is 0.

Note: the recipients are aa, Aa, or AA. The solid blue points on the graph are averages over many randomly chosen recipients, whose individual genotypes are shown by the open blue circles.

Note: the frequency of allele A in the population affects the intercept of the line (where it crosses the y-axis) but not the gradient.

Regression Relatedness Mother to Son

Here we compare the genotype of a haplodiploid female donor individual with her son.

The son is haploid so can only have genotypes a and A, which score 0 and 1. (0% and 100% of his genotype at that locus is A.)

The son gets all his genes from his mother. If the mother is AA her son must be A. If the mother is aa her son must be a. If the mother is Aa, then half her sons are a and half are A. the average score (shown) is 0.5.

The gradient of the regression through these points is 1.

The regression relatedness is 1.

Regression Relatedness Mother to Daughter

Note: Allele A has frequency 2/3 in population.
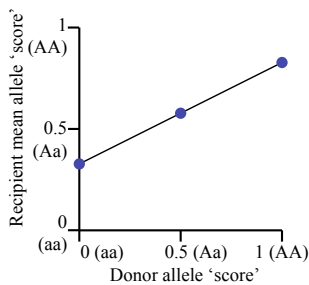
Here we compare the genotype of a haplodiploid or diploid female donor individual with her daughter.

The daughter gets half her genes from her mother and half from her father. If we assume that the father and mother are unrelated (outbreeding) then the genes from the father are essentially taken at random from the population.

If mother is AA, daughter gets one A allele from her. From father she gets the average of the population: A with probability 2/3 and a with probability 1/3. Her total score is therefore 1.666/2 =0.833.

If mother is aa, average daughter score is 0.666/2 = 0.333. If mother is Aa, daughter score is 1.166/2 = 0.583.

Gradient of regression is 0.5.

Regression Relatedness Mother to Daughter

Note: Allele A has frequency 2/3 in population.

↑ Mother's contribution   ↑ Father's contribution
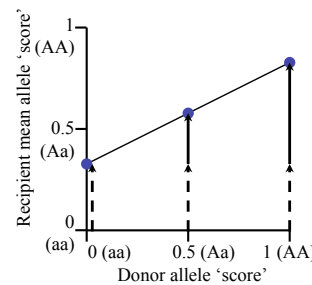
If anyone is struggling with the previous slide this may help.

The average contribution from the father is an A allele with probability 2/3 and an a allele with probability 1/3. These probabilities are not from any one father, who must be either a or A and so can only contribute either a or A. They are from many sets of parents all in the same population. On average, 2/3 of the fathers are A and 1/3 a.

The graph now also shows the average contribution of the father (an A allele with probability 2/3 giving a score of 1/3), and the contribution of the mother to the overall score of the daughter. Essentially, the random genes from the father halve the gradient.

Regression Relatedness Mother to Daughter
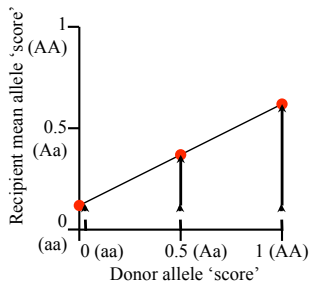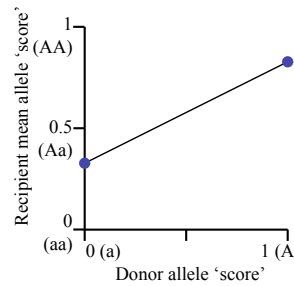

Note: Allele A has frequency 1/4 in population.

Mother's contribution | Father's contribution

This figure is the same as that before except the frequency of allele A in the population is now only 1/4.

Note that the gradient remains 0.5 even though the intercept has changed.

The father's average contribution to the A score has diminished to 1/8. The mother's contribution is unchanged.

Regression Relatedness Son to Mother

Note: Allele A has frequency 2/3 in population.

We now consider the reverse situation from a few slides ago, with a donor son and a receiver mother.

The son receives all his genes from his mother but she only gives half her genes to him. This is because she is diploid and he is haploid. In the mother is outbred her two alleles at a locus will not be correlated.

If the son is A the mother can be either AA or Aa. On average, 2/3 will be AA and 1/3 Aa. So the average score of the mothers is $(1.666/2) = 0.833$. If the son is a the mother can be either Aa or aa. Here average score is $0.666/2 = 0.333$.

The gradient is 0.5, so regression relatedness is 0.5.

This shows that the regression relatedness of son to mother is different from mother to son.

Regression Relatedness Full Sisters
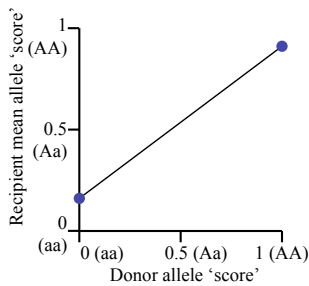
Note: Allele A has frequency 2/3 in population.

The gradient is 0.75.
Regression relatedness is 0.5.

The next slide shows how to work it out.

Regression Relatedness Full Sisters

It is a bit trickier to work out the relationships between sisters. A more detailed treatment is given in the long handout. Here we will just consider the cases of AA and aa donors for full sisters.

Full-sisters have the same father. Their father is haploid so both receive the same allele from him, either A or a. So if the donor is AA she must have received an A allele from her father, and her full sister must have the same A allele. Similarly, if the donor is aa she must have received an a allele from her father, and her full sister must have the same allele.

Now consider the maternal genes. If the donor is AA, she also received a A allele from her mother. There is a 50% chance that her sister will also receive this allele, and a 50% chance that her sister will receive the other allele. The chance that the other allele is A is the frequency of A in the population (2/3), assuming the mother is outbred. Thus, the sister has a $0.5 \times 1 + 0.5 \times (2/3) = 5/6$ chance of receiving an A allele from mum.

Overall, the allele score of the full sister is $0.5 \times 1 + 0.5 \times 5/6 = 11/12$.

If the donor is aa she received an a from both parents. The chance that her full sister received an A allele from their father is 0. The chance that she received an A allele from the mother is $0.5 \times 0 + 0.5 \times (2/3) = 2/6$.

Overall, the allele score of the full sister is $0.5 \times 0 + 0.5 \times 2/6 = 2/12$.

Learn These Regression Relatednesses

Donor	Recipient	Regression Relatedness
Female	Full-sister	0.75
Female	Half-sister	0.25
Female	Mother, Daughter	0.5
Female	Son	1
Female	Mother's son (Brother)	0.5
Female	Full sister's son (Full nephew)	0.75
Female	Half-sister's son (Half nephew)	0.25
Male	Sister	0.25
Male	Daugher	0.5
Male	Brother	0.5
Male	"Son"—mate's son	0

Hints: 1. There is no difference in relatedness if you switch donor and recipient if they are the same sex. Thus, relatedness of mother donor to daughter recipient is the same as daughter donor to mother recipient. There is a difference, however, if donor and recipient are of different sexes. 2. A female's relatedness to another female is the same as her relatedness to that female's son.

Regression Relatednesses. Notation

Notation: when writing regression relatednesses in formulae use the notation $b_{rd,i}$ where r is the recipient, d the donor, and i the colony or colonies or population you are referring to.

For example $b_{qw,i}$ could mean "the regression relatedness of the workers (donors) in colony i to the young queens (recipients) being reared in colony i".

Because of haplodiploidy $b_{male,female} \neq b_{female,male}$ so it is important to consistently put the donor second when donor and recipient are of different sexes.

However, relatednesses within a sex are the same when donor and recipient are switched. For example, $b_{daughter,mother} = b_{mother,daughter}$

Life for Life Relatednesses

In most books and articles relatedness is given in the life-for-life format. Essentially, this format combines regressions relatedness with sex-specific reproductive value.

It is difficult to use this format when studying sex ratio optima when there is male production by workers.

It is also easier to understand how the theory is developed when keeping relatedness and sex-specific reproductive value separate.

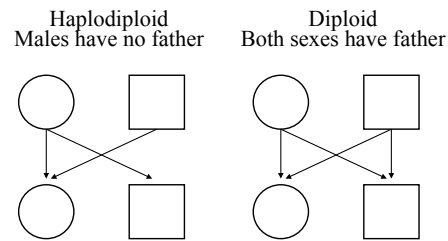For that reason, this course uses the regression relatedness format.

Life for Life & Regression Relatednesses

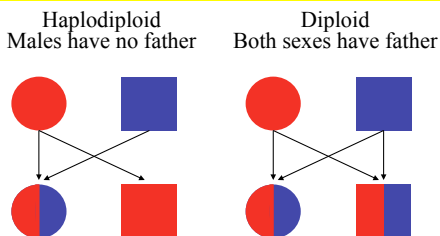| Donor	Recipient	Relatedness: Reg	Life for Life
Female	Full-sister	0.75	0.75
Female	Half-sister	0.25	0.25
Female	Mother, Daughter	0.5	0.5
Female	Son	1	0.5
Female	Mother's son (Brother)	0.5	0.25
Female	Full sister's son (Full nephew)	0.75	0.375
Female	Half-sister's son (Half nephew)	0.25	0.125
Male	Sister	0.25	0.5
Male	Daughter	0.5	1.0
Male	Brother	0.5	0.5
Male	"Son"—mate's son	0	0

The differences occur when we consider relatedness between sexes. Life for life is half regression when the donor is female and the recipient male (e.g., female workers rearing males), and double regression when the donor is male and the recipient female (e.g., father rearing daughter—which does not happen).

Sex-Specific Reproductive Value

Gene Transmission Between Generations

Haplodiploid
Males have no father

Diploid
Both sexes have father

Gene Transmission Between Generations

Haplodiploid
Males have no father

Diploid
Both sexes have father

Gene Transmission Between Generations

Haplodiploid
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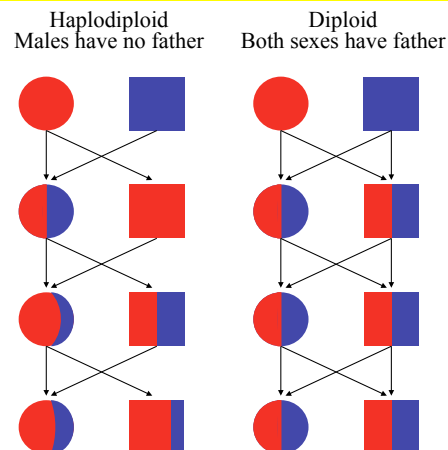
Worker Reproduction & Gene Transmission

Haplodiploid
Males have no father

Diploid
Both sexes have father

Eusocial Haplodiploid
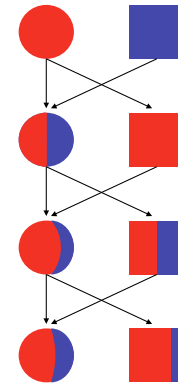Males workers' sons
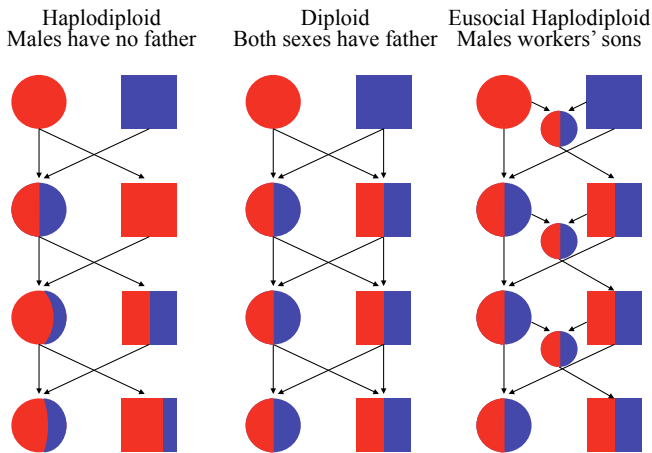
Worker Reproduction and Gene Transmission

Eusocial haplodiploid
all males queens' sons

Equations can represent the diagram on the left showing gene transmission from one generation to the next. p_f and p_m mean the gene frequency of the "red" genes in females and males; * means in the next generation.

$$p^*_f = p_m/2 + p_f/2 = (p_m + p_f)/2$$

$$p^*_m = p_f$$

Iterate these equations by putting the newly calculated values of p^*_m and p^*_f back into the right hand side to calculate p^*_m and p^*_f over and over again for generations 3, 4, 5 etc. In this way we can follow gene frequency changes over many generations. For example, if we say that p_f in generation 1 = 1 and p_m = 0 (i.e., initially genes in females are all "red") we can determine where the red genes end up. They end up in both sexes, with each sex having more than half its genes red.

Reproductive Value V

generation	a) males	p(m)	p(f)	b) males	p(m)	p(f)	c) males	p(m)	p(f)
1	1	0	1	0	0	1	1	0.5	0	1
2	1	1	0.5	0	0.5	0.5	0.5	0.75	0.5
3	1	0.5	0.75	0	0.5	0.5	0.5	0.5625	0.625
4	1	0.75	0.625	0	0.5	0.5	0.5	0.6094	0.5938
5	1	0.625	0.6875	0	0.5	0.5	0.5	0.5977	0.6016
6	1	0.6875	0.6563	0	0.5	0.5	0.5	0.6006	0.5996
7	1	0.6563	0.6719	0	0.5	0.5	0.5	0.5999	0.6001
8	1	0.6719	0.6641	0	0.5	0.5	0.5	0.6	0.6
9	1	0.6641	0.668	0	0.5	0.5	0.5	0.6	0.6
10	1	0.668	0.666	0	0.5	0.5	0.5	0.6	0.6
11	1	0.666	0.667	0	0.5	0.5	0.5	0.6	0.6
12	1	0.667	0.6665	0	0.5	0.5	0.5	0.6	0.6
13	1	0.6665	0.6667	0	0.5	0.5	0.5	0.6	0.6
14	1	0.6667	0.6666	0	0.5	0.5	0.5	0.6	0.6
15	1	0.6666	0.6667	0	0.5	0.5	0.5	0.6	0.6

V(f)/V(m) = 2.0002   1   1.5

generation
proportion of males in whole population that are queens' sons
proportion of genes in whole population initially in females (gen 1) now in males
proportion of genes in whole population initially in females (gen 1) now in females
V(f)/V(m) is the relative sex specific values of females to males, = p(f)/(1-p(f))

Reproductive Value V

The slide before is from an Excel spreadsheet set up to iterate the two equations from the slide before that.

The first column is the generation, starting with generation 1. The other columns represent three simulations for cases in which proportions 1, 0, and 0.5 of the males in the population are queens' sons "males".

The two columns to the right of "males" represent the frequency of red genes in males, p(m), and females, p(f), of that generation. The frequency is initially set, in generation 1, to 0 in males and 1 in females.

The frequencies change generation to generation and eventually stabilize. In the first simulation ("males" = 1), they stabilize at 2/3 in both sexes. This tells us that genes in females contribute 2/3 to the gene pool of the population while males contribute the rest, or 1/3.

The ratio of the sex specific reproductive values of females and males, V(f)/V(m) is, therefore, (2/3)/(1/3) = 2.

The simulation for "males" = 1 stabilizes after one generation, with 0.5 in both sexes. This is the same as the diploid situation. The simulation for "males" = 0.5 shows that the ratio of the sex specific reproductive values of females and males, V(f)/V(m), is 1.5. In other words, it is (1+proportion of males that are queens' sons).

Life for Life Relatednesses

The sex-specific reproductive value of females to males is a ratio, V_F/V_M. When all the males in the population are workers' sons the ratio equals 2. It is sometimes convenient to think of this as meaning that $V_F = 2$ and $V_M = 1$. But it is also fine to think of it as $V_F = 1$ and $V_M = 0.5$. Both are the same as the ratio V_F/V_M is the same. If we take $V_F = 1$ and $V_M = 0.5$, we can now see that life-for-life relatedness is basically regression relatedness x sex-specific reproductive value.

Kin relationship	Reg. relatedness	LfL relatedness
Worker to full sister	0.75	0.75 x 1 = 0.75
Worker to brother	0.5	0.5 x 0.5 = 0.25

Sex-Specific Mating Success

Not all individuals of same sex have same mating success.

Some males many offspring, others none.

What about the two sexes? Can members of one sex have greater mating success than the other?

Consider a population with 2 females per male.

If each female mates with just one male, then, on average, each male mates with two females.

If each female mates with two males, then, on average, each male mates with four females.

If a male can only mate once, then half the females remain unmated.

Each (only females in Hymenoptera) offspring has exactly one father and one mother.

On average, a male has twice as many sets of offspring as a female when sex ratio is 2F:1M.

You can work though this example for different ratios, such as 1 female per 2 males.

In many eusocial insects males and queens are not same size.

Queens are usually larger and require more investment.

This must be accounted for when we consider mating success.

When we do this, we can see the overriding importance of the allocation sex ratio not the numerical sex ratio.

Cost female = cost male
Numerical sex ratio is 1F:1M
Allocation sex ratio is 1F:1M

Cost female = 2 cost male
Numerical sex ratio is 1F:2M
Allocation sex ratio is 1F:1M

Cost female = 0.5 cost male
Numerical sex ratio is 2F:1M
Allocation sex ratio is 1F:1M

In all three examples above, the sex-allocation ratio in the population is 1F:1M. The mating success is equal per unit allocation in either sex, even though the numerical sex ratios differ.

Study the previous slide until you understand why the allocation ratio is more important than the numerical ratio. The basic theory for determining optimal sex ratios makes predictions about the sex allocation ratio to the two sexes, not the numerical ratio of the two sexes.

Consider what would happen if the numerical ratio were the key. If the optimum numerical ratio was 1F:1M, then females who made small sons would be at an advantage, as they would have spare resources to make more daughters. So males would get smaller. But equally, females who made small daughters would have spare resources to make more sons. So females would get smaller. It's a logical impossibility.

Kin Value = Regression relatedness x SSreproductive value x SSmating success. Consider two simple examples: the kin value of the males and the queens reared in a colony with a single queen mated to a single male.

Relatedness of workers to males, b_{mw} = 0.5
Relatedness of workers to queens, b_{qw} = 0.75

All the males are queens' sons, V_F/V_M = 2
(we can say $V_F = 2$ and $V_M = 1$; What is important is the ratio of V_F/V_M or M_F/M_M)

And the sex-allocation ratio is equal, M_F/M_M = 1
(we can say $M_F = 1$ and $M_M = 1$)*

The kin value of a male is $b_{mw}V_M M_M$ = 0.5 x 1 x 1 = 0.5
The kin value of a female is $b_{qw}V_F M_F$ = 0.75 x 2 x 1 = 1.5

Kin Value

The previous slide shows that a female (a young sister queen who is the daughter of the mother queen) has three times the kin value of a male (a brother) to the workers. We will later see what implications this has on queen-worker conflict over sex allocation.

But can you already see what may happen. What will the optimum sex ratio of the workers be? Male bias, female bias, or equal?

How would differences in the sex allocation ratio to males versus females in the whole population affect things?