Sexual Reproduction, Sex, and Sex Ratios
Ethology and Behavioral Ecology

These are favorite topics, in part because they involve more mysteries than you might think

Why is there sex? The oldest form of reproduction is by simple fission and mitosis (clonal reproduction) and it works well enough. Moreover, there are some obvious problems with sexual reproduction:

      1. Sex requires a certain additional amount of time and energy and it may also increase exposure to predators

      2. If you are a member of a rare species it may be very hard to find the opposite sex. A classic example is a potted cycad plant in Britain's Queue Gardens; this is a male and is apparently the last remaining member of its species!

      3. Some individuals are less successful than others regardless of other general fitness attributes.

      4. Your mate may desert you and thereby force you to raise the young (most common a problem for females, but not always) or you might be cuckolded by another male (obviously usually a problem for males) and unknowingly raise his young

      5. Sisyphean genotypes -- sex breaks down especially fit combinations of genes just as readily as it breaks down bad ones. Think of sexual species as having to perform Sisyphus's task over and over again.

      6. Altruism vs. individuality sex produces diversity, which, as we have seen, is the enemy of cooperative behavior.

There is another problem but it is often misstated. In asexual populations, the offspring are 100% related to the parent. However by contrast in most sexual species, the offspring are only 50% related. On the face of it fitness is lowered by 50% -- so for sex to evolve each (in a sex -- no sex system) each individual must reproduce 2X on the average of those of an asexual system. However, this is not exactly correct as stated. In fact, one might expect that in a sexually reproducing population that the gene for sexual reproduction would be fixed. Thus, since this "gene" is the only thing that matters with respect to the maintenance of sexual reproduction, all individuals are 100% related at this locus to their offspring. Here is a more correct way of looking at this:

Imagine a situation where a presently sexually reproducing diploid population has:
      (i) A sex ratio of 50:50
      (ii) The cost of producing members of either sex is the same
      (iii) Resources for reproduction are limited and on the average, each female is able to produce 2 offspring
      (iv) There is no male investment beyond mating

> **?** Do these look like reasonable assumptions about an animal population? They are not true in all populations and as we work throughout the next several weeks of material be thinking about how different systems might affect the model we are about to look at.

Assume that a mutant **female appears who is asexual**.

      (i) For the sake of argument, let's also <u>assume that she produces only female offspring</u>.

      (ii) Furthermore,<u> her offspring are no more expensive to produce than those of the sexual females</u>

      (iii) <u>Except for the locus that controls her ability to reproduce asexually, she is the same as the other females</u> -- she has th<u>e same competitive abilities</u> and ability to funnel energy and material into offspring. Thus, she will **<u>on the average have 2 offspring in her life</u>**.

      (iv) Assume that the <u>allele for asexual reproduction is dominant</u> over the one for sexual reproduction.

? Why not a female that produces male and female offspring? Male only? Why is this the only type of asexual female that is likely to persist?

What is the likely genotype of the first asexual individual? What will be the genotype of her offspring? What will happen to them?

(To make this simple <u>assume X Y sex determination as in mammals.</u> Furthermore, to make this realistic (but less simple), <u>assume that she produces eggs by meiosis (they are n) but that they develop by doubling their number to 2n </u>on the first division, after that division is normal. Alternately, assume that she produces eggs by meiosis and that her daughters develop as haploid individuals and produce eggs by mitosis (both of the these mechanisms occur!)

Assume that we start with 101 individuals: **50 sexual males, 49 sexual females** and **1 asexual female**. <u>Assume that there is no mortality of the offspring</u> i.e., that the population is expanding.

      1. Calculate the frequencies of the sexual allele (a) and asexual (A) alleles in the parental generation; call them p and q

      2. Continue to calculate the frequencies for two more generations.

Answers: P $p = 0.99$, $q = 0.01$
         F_1 $p = 0.98$ $q = 0.02$
         F_2 $p = 0.96$ $q = 0.04$
         F_3 $p = 0.925$ $q = 0.075$
         F_4 $p = 0.86$ $q = 0.14$

Notice that the frequency of the asexual allele is essentially doubling each generation -- while this will not go on forever, eventually the allele will totally dominate the population!

? Suppose that there was no difference in mortality between the sexual and asexual types but that the population was fixed at 100 individuals (more realistic than our example if we choose to assume that many natural populations are operating near their carrying capacity, K -- or that even "r-selected" species (those that often operate well below K and

are selected for rapid reproduction) will nevertheless eventually reach K). Will the asexual allele under these conditions spread more or less rapidly? How would you calculate this?

Suppose that parental care was important in this species. Further suppose that individuals alone were capable of producing an average of 1 surviving offspring while those that had a helper (which could be a male) produce an average of 2.1 surviving offspring.
What will happen now? Who should males help? Why?
Should asexuals help? Who? When?

Note once again that it is not absolutely correct to say that the asexual allele increases because the offspring are 100% related while in sexual individuals they are only 50% related. The reason is that in both cases at the sexual locus the individuals are 100% related to their offspring at this locus
      (a) It is easy to see in the case of the asexuals -- if they are either haploid or diploid you must realize all would have the same genotype since they are a clone and that genotype results in an asexual female.
      (b) However, the sexuals are also 100% related
            (i) Every sexually reproducing individual is homozygous
            (ii) All sexually reproducing individuals contain this allele by common descent (think of it as being in this case in the uncorrelated and correlated genome of these individuals).
            (iii) While it is true that each offspring will receive only one of these alleles for each parent, the locus is entirely inbred and the offspring will instead get another copy of the allele from the other parent.
            (iv) Thus, the offspring will contain two copies of the same allele that are identical to the two copies in each parent; thus at this locus (and it is the one that we are considering here) the parents and offspring of sexually reproducing individuals are 100% related! -- the other copy comes from the other parent.
            (v) Therefore, this is a special case of Hamilton's description of correlated and uncorrelated genomes -- here f = 1.0 and which is the same as assuming for this locus that $r_{ij} = 1.0$.

The other thing that is commonly said is that sexual reproduction can spread genetic novelty through a population more quickly than asexual reproduction. That is true up to a point.
- First keep in mind that novelty enters asexual populations only through mutation and sexual ones through both mutation rates (which are low in all species) and recombination (which is common).
- Next, remember that generational time is an important variable. Changes, whether by mutation or recombination, are only added at reproduction. Moreover, generational time is assumed to be the same for both asexual and sexual individuals that belong to the same species.
- When computer simulations are run, it is found that large populations of asexual organisms do quite well in the face of certain types of environmental

change, especially if it is non-cyclic. This should surprise no one -- there are lots of successful asexual species and they have been around for a long time.

So, **why is sexual reproduction as common as it is**?
The big answer appears to be that sexual reproduction is a means to **hedge your bet.** When do you need a hedge? Well, the answer is clearly it will be needed in cases where there is considerable environmental uncertainty. But which part of the environment?
(a) Abiotic -- contrary to what you might think, asexual reproduction is relatively more commonly associated with ephemeral habitats and those that are particularly severe. Perhaps this is an adaptation or consequence of r -selection.

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r - selection refers to the selection for species that are capable of rapid colonization of a habitat. Such species are usually very good dispersers, they put large amounts of energy and resources into reproduction and not into development of systems for competing with other individuals, the have high intrinsic rates of increase which are achieved by short generations and large numbers of gametes and zygotes or cell divisions and if sexual, they are often semelparous. The "r" in the r-selection refers to the intrinsic rate of increase of the population (see earlier notes) and the exponential growth of a population.

(b) Biotic -- on the other hand, sex is most common where there are severe biotic interactions; i.e. where organisms are more commonly of the "K-selected" type.

K-selected organisms are specialized as excellent inter and intra-specific competitors. They tend to have longer life spans, be less adapted for dispersion, are iteroparous, often have some form of parental care, and they tend to have lower intrinsic rates of population growth. The "K" refers to carrying capacity -- these species are specialized to operate in situations where their populations are at or near K.

A particular example showing the sorts of biotic interactions have to do with long-term cyclic changes in the abiotic environment. The term "**Contrariness**" is often applied so such environments. One example was originally put forward as a model by Clarke and deals with cyclic relationships between host and parasite species -- as the host changes so must the parasite and vice versa-- the changes in one species change the environment for the other:

Cyclic Relations Between Parasites and Hosts

Host Genotypes
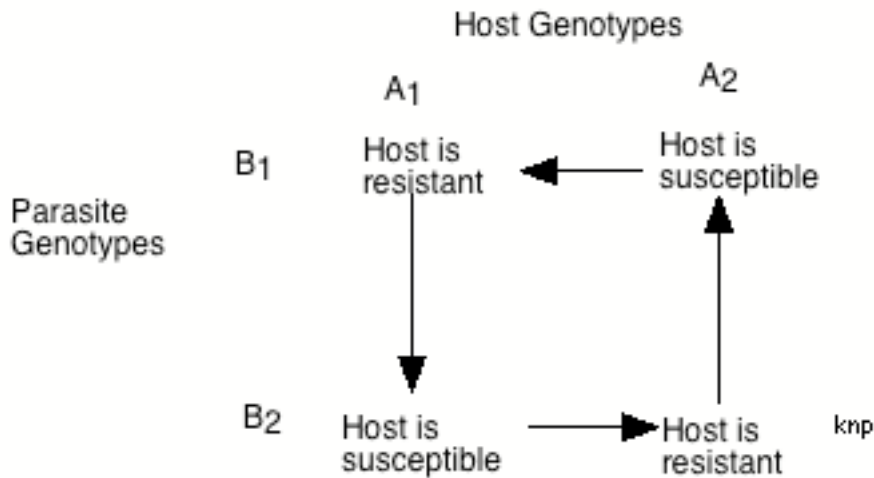
(ref. Clarke 1976 – *Genetic Aspects of Host Parasite Relationships, Symposia for the British Soc. of Parasitology* 14, 87)

Notice in the model above that <u>fitness is frequency-dependent</u> -- when common in one species, a response is evolved in the other (think of the communication model we learned earlier).

How did sex evolve? The answer is that it almost certainly came from excision repair mechanisms that appeared early in the history of life. In excision repair, mistaken pairings are removed from DNA sequences. From this it is a short step to taking DNA from one source and occasionally substituting this for DNA already in the cell. Such a phenomenon occurs with **transformation** in bacteria -- DNA from dead bacteria can, at a low rate, become incorporated in place of similar bits of DNA in a living cell thereby changing it genetically and producing a sort of genetic recombination.   Bacteria apparently later developed conjugation as a more efficient means of recombination -- in conjugation, sections of DNA are exchanged or given from one cell to another.
      Where do we go next? According to Parker et al (1972 -- J Theor Biol 36:529) there are two possible general arrangements for sexually reproducing species:
      First, we assume that simplest arrangement is for sex to involve just two individuals at a time. There is no reason in principle that it could not involve more, only this is likely.

? What are some of the reasons that multiple partners (more than two required to complete the basic recombination) is not a likely system? You should be able to identify reasons based on probability of individuals finding partners and on the nature of the repair mechanism in DNA.

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    1. **Isogamy** - here there are <u>no separate sexes</u> per se but there is sex.
        a. Genetic contributions of both sexes is equal

b. The material contributions ("parental investment") of both partners are equal. Thus there is no morphological differentiation of gametes

c. There must be some way to determine difference however -- or at least it would seem advantageous to have such a mechanism. The reason is that there is no advantage to mating with a clone of yourself -- in fact, if one of the main reasons of sex is to increase recombination then you would definitely expect to see the evolution of mechanisms that create outbreeding.

1. One such mechanism is to use **mating strains**.

a. These are identifiable lines that will not breed with each other (or in some cases with closely related mating strains).

b. They only breed with other, generally distantly related strains.

2. These are not sexes -- they are adjuncts to sex by forcing outbreeding. In most species that have these, there are many distinct strains.

Paramecium -- is like most Ciliophora -- it has a highly derived but very interesting morphology. In conjugation in *Paramecium* ere the gametes are essentially the haploid micronuclei that are transferred to between conjugating individuals. There is essentially no net transfer of cytoplasm during the conjugation. In one sense the parents are also the gametes since after the transfer the arriving nucleus fuses with their remaining micronucleus (the actual syngamy in this case) Thus, the concept of gamete is rather different in these organisms -- the nuclei are the gametes.

? What then is the purpose of inbreeding -- is it essentially to gain the advantages associated with asexual reproduction?

2. **Anisogamy**: assume that instead in some species there is variation in the size of gametes produced. We will not get into how this gets started and maintained but we will define the differences:

(a) Female is the type that produces a few relatively large gametes; put another way, it is a strategy that produces a small number of expensive gametes.

(b) Male therefore produces many small gametes; investment in each individual gamete is relatively low and therefore with a given amount of energy and material many can be made.

Note that in anisomgamy the amount of genetic material donated by the two sexes to the new individual is essentially the same. Thus, the offspring is related equally to each of its parents.

Characteristics of the Sexes:
Males --physiologically there is usually little investment compared to females; this is driven home by the fact that generally males can have successful sex many times.

By contrast, females have fewer expensive gametes. Once these are fertilized they are not easily replaced. Females can have sex as often as they might wish but additional matings usually has little potential to increase their fitness.

Bateman (1948) looked at this with *Drosophila* that possessed well-defined genetic markers:
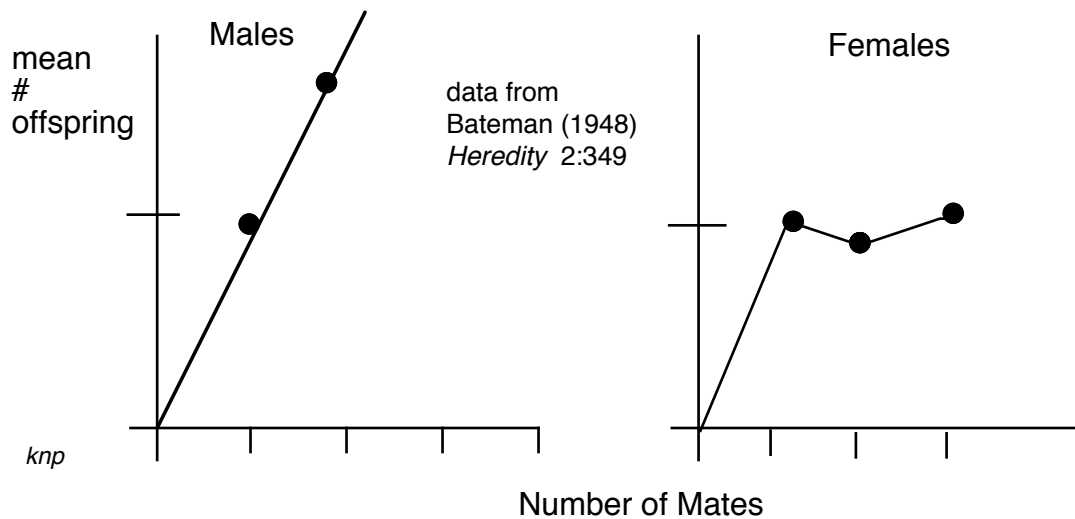

Notice that in males success continues to increase (for a while at least) with increases in the number of partners whereas female success is essentially maximum with one mate.

Actually if considered over enough individuals females often get slightly higher fecundity if they mate with perhaps two males to decrease chances of genetic incompatibilities.

One other point about Bateman's data. Does it mean that the average male will have more offspring than the average female?
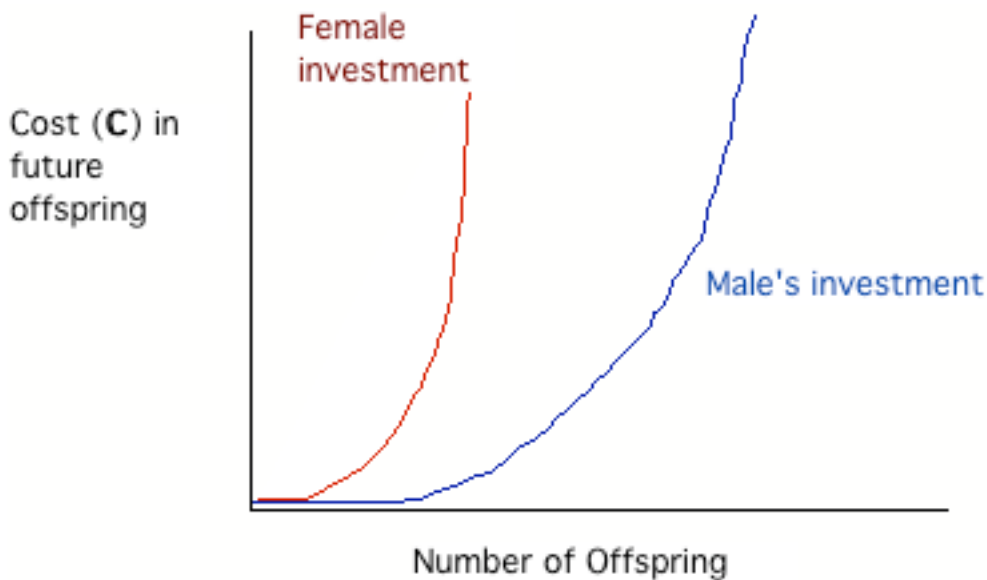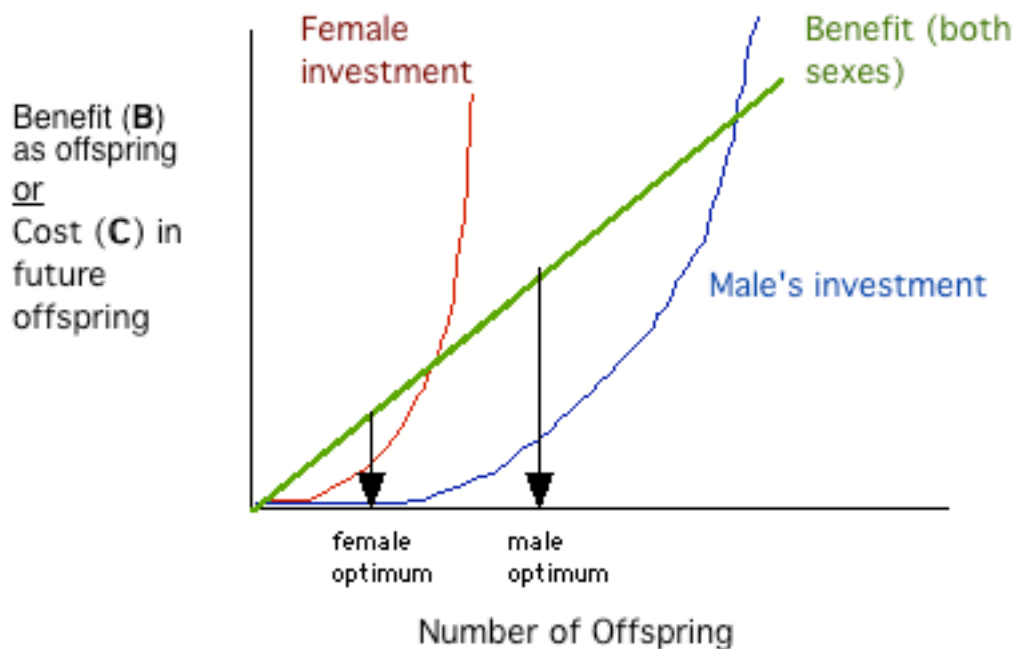NO! But it does mean that some males will have many more than others.
Let's look at a bit more data in regards to differences between males and females. This is from Trivers. This will be an optimality model where we will look for the best number of offspring for each sex. First lets generate a benefits curve - it'll be a straight line since the decision variable is also the currency:

Benefit (offspring) — Offspring — Benefit — Cost (future offspring)
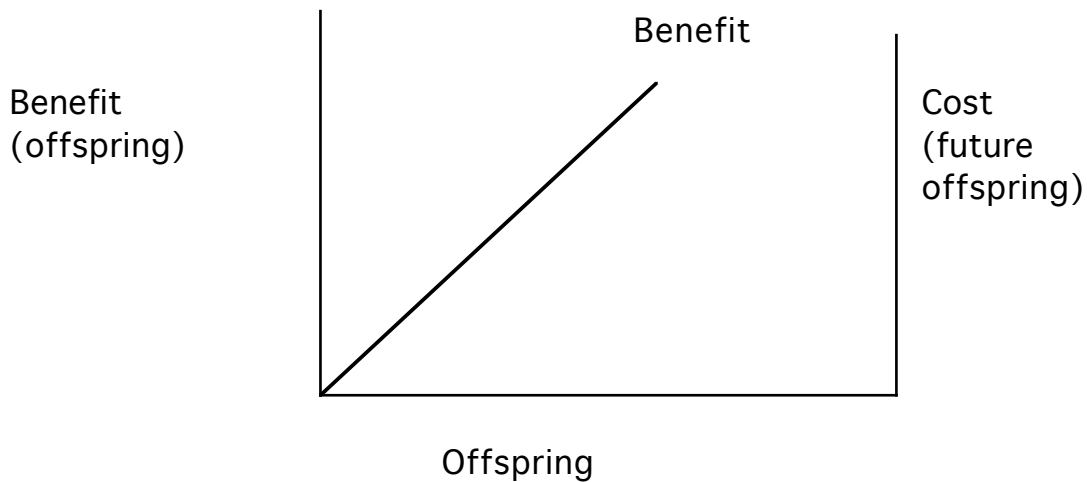
What about costs?

Female costs rise more rapidly than do male -- a harder toll is taken on her body (if we assume both the cost of gamete/young production and parental care as vs. parental care only). The shape of the curve will be a curve since over part of a range of numbers of offspring there is little cost -- we have seen this earlier with birds -- but eventually a point is reached where the costs become a greater and greater burden. By contrast, the cost in males rises more slowly at first since gametes are so cheap to produce:

Cost (**C**) in future offspring — Female investment — Male's investment — Number of Offspring

Female investment
Benefit (both sexes)
Benefit (**B**) as offspring or Cost (**C**) in future offspring
Male's investment
female optimum
male optimum
Number of Offspring

We will see in coming classes that the fundamental asymmetry shown above is probably an important basis to indiscriminate male sexual behavior as compared to highly discriminating behavior by females.

Will selectivity be important to males? Sometimes, we will see, but often, no.

On the other hand, bad choice weights heavily on females.

Thus: males -- fast and loose
females -- only to the correct stimuli -- all she needs is one male

The Sex Ratio
What is the best ratio of individuals of each sex? One other way to phrase this is to ask why are there so many males. Let's think about this:

Suppose that we have a sexually reproducing species and males and females are the same cost (through the period of parental investment).
Now recall that both sexes contribute equally to the next generation genetically but the female makes the main material investment. Thus, the answer to the question of "through which sex are more of your genes spread?" is "neither".
Now suppose that most females produce daughters to sons at a ratio of 3:1.
If this is the case males are on the average 3X as successful as females. However, for reasons outlined earlier when we considered asexual vs. sexual reproduction the whole population is more productive since females are more productive than males -- we really only need a few males around.

Now, a mutant female appears who produces daughters and sons at a 1:1 ratio. Her daughters are just as successful as the general pop but her sons are 3X as successful since the overall sex ratio is still close to 3:1.

Let's look at how each of the females does:

We assume that both have a total of 4 offspring

The "normal female" has 3 female offspring + 1 male offspring. Each of her daughters also has 3 and 1 (total 9 female and 3 male grandchildren from her daughters) and her son has 9 female and 3 male offspring. This gives a total of:

24 grandchildren (18 female and 6 males)

Now the mutant has 2 female and two male. Her daughters produce 2 daughters each and two sons each for a total of 4 of each. On the other hand, her two sons, being males, are in this case three times as successful and they produce a total of 6 daughters and 6 sons each. Thus she has a total of 8 + 24 = 32 total offspring (vs. 24 for the 3:1 female) and obviously the gene for 1:1 will spread

> Satisfy yourself that if a mutant who produces more sons than daughters appears that her genes will not spread.

In the 1930's Sir Reginald Fisher looked at all of this and came up with the following rule for determining the <u>sex ratio at the end of the period of parental investment</u>. It is based on the<u> idea of equal allocation of resources to both sexe</u>s and it<u> assumes that parents are equally related to all of their offspring</u>:

females * cost female = # males * cost of males

Or, expressed as ratios:

sex ratio = cost ratio

 # males / # females = cost female / cost male

Fisher's rule assumes or implies the following:

      1.**It IS INDEPENDENT OF THE MATING SYSTEM**. In different mating systems such as monogamy, polygyny, and polyandry the variance in reproduction found within each sex changes. However, in each case the average reproduction of males compared to females must be equal since the offspring are 50% related to each parent; thus it doesn't matter if, for instance the system is polygynous and some males do extremely well and others do not reproduce -- the result is still that male reproductive success equals that of females.
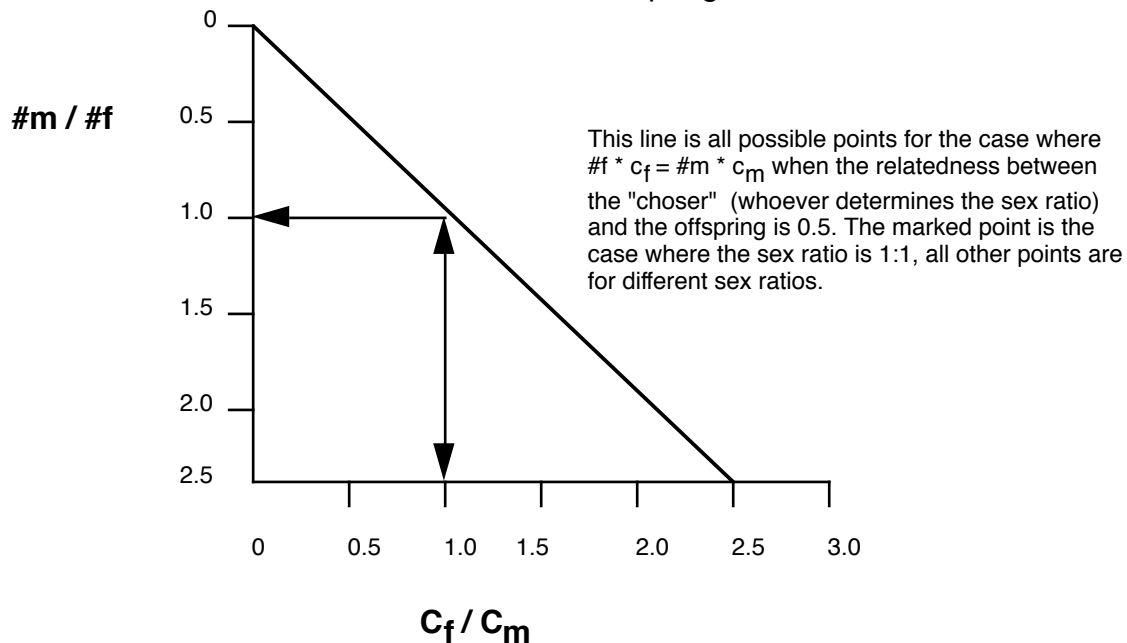
      2. **The population is large and outbreeding -**- Fisher assumes that parents are competing against each other when they allocate resources into male and female offspring. If the population were to be inbred, competition would tend to be relaxed for reasons we have already discussed in detail earlier in the course.

3. **Differential mortality or differential effects on the sex ratio matter up through the period of parental investment** --It is not uncommon for the sex with the higher death rate to be less costly per individual that is born but it may be the more costly per individual that survives -- it is the latter number that matters when determining the stable sex ratio. As a result, when there is differential mortality, the sex that dies out tends to start with a relatively high primary proportion, this decreases to the Fisher ratio by the time parental investment is terminated.

4. The population as a whole must have the sex ratio predicted by Fisher -- what matters is the average payoff per investment be equal in the two sexes. Thus, it is possible for alleles that favor different sex ratios to coexist as long as they tend to balance each other out.
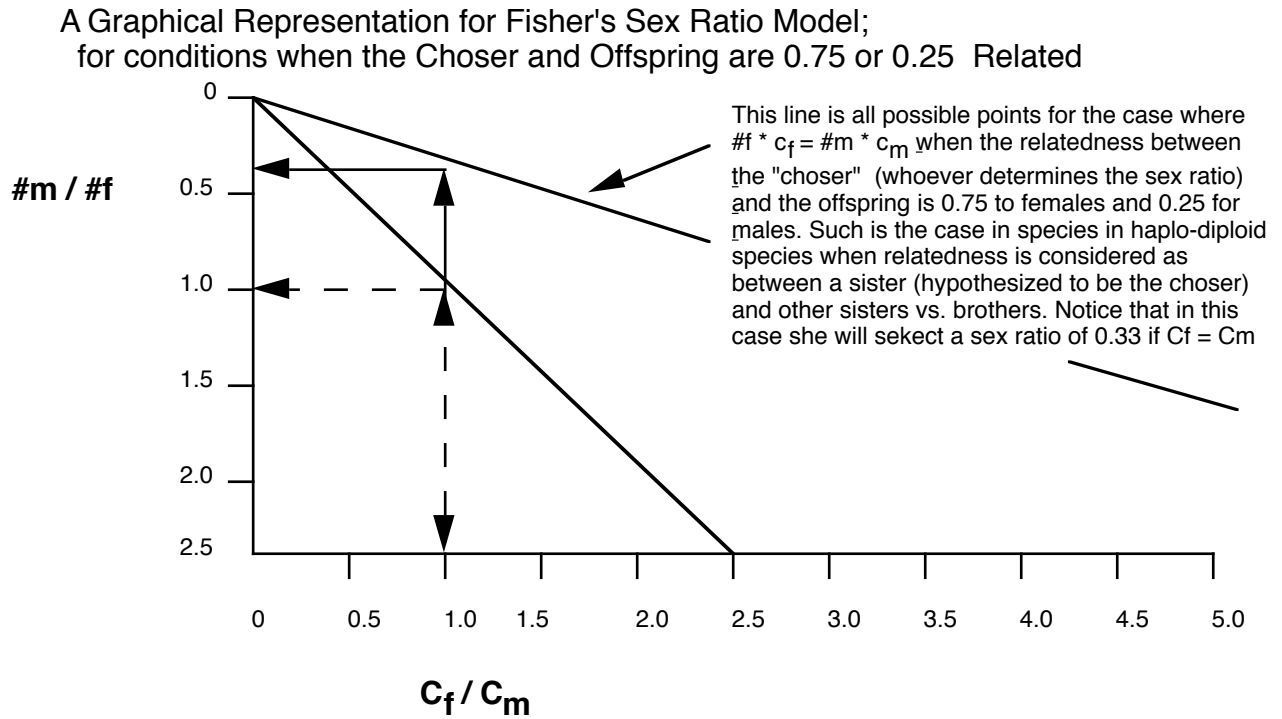
We can plot Fisher's rule by putting the sex ratio on the Y-axis and cost ratio on the X-axis. It is convention to show the sex ratio as decreasing towards zero as one moves up the y axis -- be aware of this or else risk some confusion:

A Graphical Representation for Fisher's Sex Ratio Model;
for conditions when the Choser and Offspring are 0.5 Related

This line is all possible points for the case where $\#f * c_f = \#m * c_m$ when the relatedness between the "choser" (whoever determines the sex ratio) and the offspring is 0.5. The marked point is the case where the sex ratio is 1:1, all other points are for different sex ratios.

(Y-axis label: **#m / #f**, values 0, 0.5, 1.0, 1.5, 2.0, 2.5)

(X-axis label: C_f / C_m, values 0, 0.5, 1.0, 1.5, 2.0, 2.5, 3.0)

The plot above shows the expected sex ratio for a series of cost ratios when the individuals who determine the sex of the offspring (the parents or one parent) are equally related to both sexes of offspring. However, what happens if someone else who has a different relationship to the offspring determines the sex ratio? Such a thing might happen in eusocial bees, ants and wasps where we have seen that the workers (female offspring) provide all the parental care. Recall that in this case they are 3/4 related on the average to the other female offspring -- i.e. to the eggs they are taking care of and only 1/4 related to their brothers. Since there is a three times greater chance that any genes they carry will be in their sisters they would be expected to skew the sex ratio towards

other sisters by a factor of three if possible. Their mother on the other hand would prefer the ratio given by Fisher's model. Here is how it looks graphically:

A Graphical Representation for Fisher's Sex Ratio Model;
for conditions when the Choser and Offspring are 0.75 or 0.25 Related

#m / #f

This line is all possible points for the case where #f * c_f = #m * c_m when the relatedness between the "choser" (whoever determines the sex ratio) and the offspring is 0.75 to females and 0.25 for males. Such is the case in species in haplo-diploid species when relatedness is considered as between a sister (hypothesized to be the choser) and other sisters vs. brothers. Notice that in this case she will sekect a sex ratio of 0.33 if Cf = Cm

$$C_f / C_m$$

Trivers and Hare (1972) tested these two models of sex determination in social and solitary species of hymenoptera. They predicted that solitary species should show ratios like those shown for Fisher's unmodified equation; they did. They then predicted that eusocial species should show ratios like those on the "low slope" curve above <u>if Hamilton's model of kin selection as the driving force behind the evolution of eusocial behavior was correct; if Alexander's parental manipulation idea was correct, the Fisher line should have been observed</u>. The result supported Hamilton. Finally, Trivers and Hare also looked at the sizes and sex ratios in ants where **dulosis** or "ant slavery" is practiced. In these species, the slaves are members of different species.   Trivers and Hare predicted that they would be unable to control the sex ratio and the Fisher ratio should be found even though these were eusocial species. That is what they found!

A final word: We assume that the sex ratio reflects a situation where the average fitness of male and female are equal -- if it were not, the system does not represent an equilibrium

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What are the situations where the sex ratio would be expected to differ from Fisher's ratio?
     INBREEDING: when closely related, there is no longer any reason to compete -- expect a female to adopt a strategy that maximizes her grandchildren -- this is best achieved as we have seen earlier by making more females. Here's a mammalian example.

Lemmings often become inbred when they recover from population crashes. It is not uncommon for what is called the X^* chromosome to appear. In this case, X^*Y gives a female and suppresses Y eggs! This biases the ratio towards females.

LOCAL MATE COMPETITION: Variations **in local population sex ratio: excess of one or the other sex often** induces increased production of the other.

This is easiest to see in <u>wasps</u> where in some species females can tell the sex of eggs already laid. A female may provision a nest in which case it would pay her to lay mostly female eggs if there is inbreeding (which there often is). A female parasitizing the nest would be best off to lay mostly male eggs.

<u>rabbits</u> -- a long wait between ovulation and fertilization gives more males -- the long wait is correlated with a lack of males.

<u>shrimp</u> -- change sex to what is most appropriate
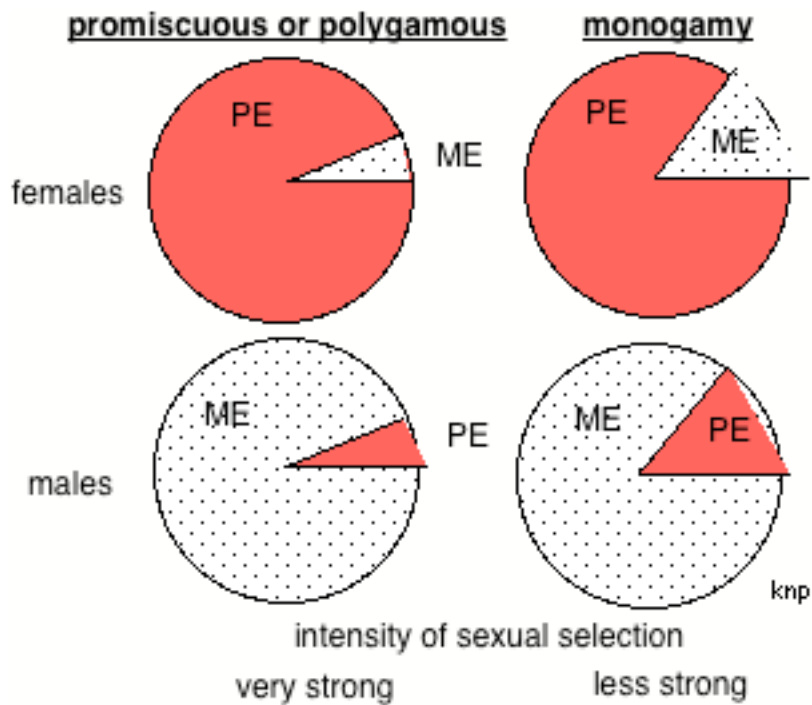
EARLY CONDITIONS -- RED DEER

Especially fit females may decide to invest more in males to increase their son's competitive ability; investment costs have therefore increased in males but the sex ratio did not decrease. Moreover there is evidence that dominant females produce a higher sex ratio (favoring males). The argument in either case is that the system is polygynous and potentially it pays to have successful male offspring more than female ones but they take heavy investment to be successful. Only deer capable of this investment will attempt it but there is potentially a large payoff.

RE = PI + ME

Where **RE** is <u>reproductive effort</u>, **PI** is <u>parental effort</u> and **ME** is <u>mating effort</u>. Should the RE be equal in both sexes? For instance, it is easy to imagine that the total energy available for reproduction might be the same. But …..

- Individuals will certainly not always be the same size; moreover, what if sex ratio is different -- do we expect similar investments per sex?
- There is a correlation between the type of mating system and how RE is partitioned

Perhaps the crucial aspect to look at is how much goes into <u>PI</u> -- defined as all reproductive effort not directed at mating but instead at reading or provisioning offspring (or protecting them).

promiscuous or polygamous   **monogamy**

females

males

intensity of sexual selection

very strong   less strong

knp

Reproductive Effort = Mating Effort + Parental Effort

Notice that in monogamy, male and female PI becomes near to equal. What would cause this?

Ecological/life history factors that force large amounts of care.

Later, when we consider game theory, we will look at this question as an evolutionary game that predicts the best strategy for males and females in different situations.