

I. The evolutionary paths to cooperation:

1. Group selection.
2. By-product mutualism
3. Kin-selected cooperation (conclusion)
4. **Reciprocity**
5. **Manipulation**

II. The mystery of sexual reproduction

Other consequences of kin-selection theory:

Understanding **conflict** between **parents** and their **offspring**

1. Freud: basic conflicts in the human family are sexual ones:
 - Penis envy, oedipal complexes, urges to kill off Dad.

2. Biology versus culture conflicts:

- Child is innately selfish and greedy.
- Socialization is imposed on him/her by society (policing of behavior).



Problems with classic analyses from the humanities & sociology:

- The explanations make no evolutionary sense.
- The same phenomena are widespread in other social animals – monkeys, squirrels, bats, even 'possums.

A clear example of conflict: **Parental Investment** in mammals, principally through the giving of food and **milk** (nursing).

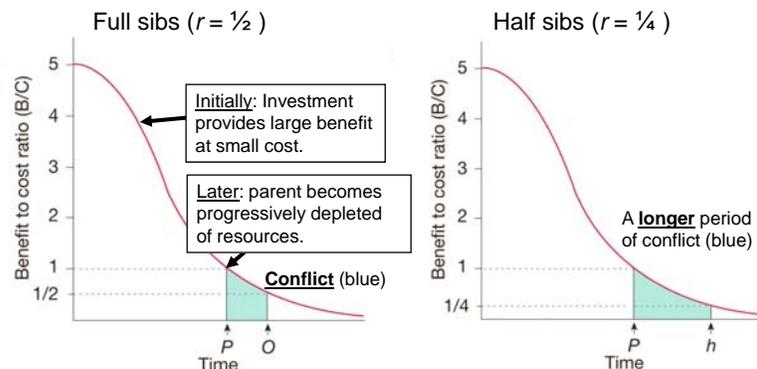
- At first, the youngster demands to be fed, and is fed willingly...
- But later, though the growing youngster continues to demand milk, the mother reduces and eventually cuts off the milk supply. Why the conflict?

Kinship and **parent-offspring conflict** (Trivers 1974)

- Whenever $r < 1$ between interacting individuals, the possibility of conflict exists.
- Parents vs. offspring: $r = 1/2$, so there is an overlap, but not identity, of self interest.
- **PARENT**: Has been selected to invest in its offspring in such a way as to maximize the number that eventually survive.
 - **Benefit** = degree to which the investment increases the offspring at hand.
 - **Cost** = degree to which the investment decreases the parent's ability to invest in other offspring, even those unborn.
 - Selected to maximize the difference between B & C, i.e. to maximize B/C
 - ...and to cut off investment when $B = C$ (i.e. $B/C = 1$)
- **OFFSPRING**: Has been selected to **de-value** the cost it inflicts compared to the benefit it receives, because...
 - it is identically related to itself ($r = 1$)...
 - but only partially related to its sibs (e.g., $1/2$ for full sibs, $1/4$ for half sibs)
 - It will be favored to **stop** asking for investment when $B/C = r$. At that point the cost will be so great that its **own genes** will suffer due to reduced parental reproduction.

Examples

- A **full sib** will be favored to stop asking for investment whenever the cost of the investment is *more than twice the benefit it receives* ($B/C < 1/2$ or $2B < C$)
- A **half sib** will be favored to stop asking for investment whenever the cost of the investment is *more than 4 times the benefit it receives* ($B/C < 1/4$ or $4B < C$)



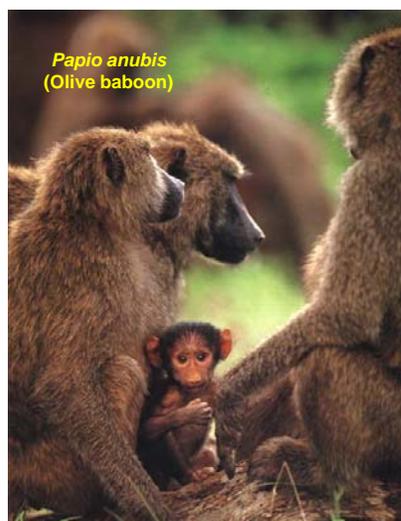
Some **general principles** to emerge about parenting from kinship theory:



Bob Trivers

- Conflict is no more due to innate selfishness of the offspring than it is due to innate selfishness of the parent.
- Where the father is the same for all offspring and $r = \text{approx. } \frac{1}{2}$ between them, the period of conflict will be relatively short.
- But when most offspring are half-sibs due to different fathers, the period of conflict will be prolonged.
- **Also:** the **older** the parent, the less its future reproductive success, reducing the cost of current investment (measured in future offspring).
 - This will select for a longer period of parental investment and reduced conflict with its offspring.
- Any support for these ideas in the real world??

An example from nature: **Baboons** of the African savannah



Olive baboon: Older mothers reject their offspring *later* than do younger mothers. (Altmann 1980)

Other examples from seagulls, red deer, and many other animals.

A special case of kin selection: **Eusociality**
(defined by sterile helper castes, overlap of generations, & colonies)

Haplodiploid sex determination: females are diploid, males are haploid, developing from unfertilized eggs. r 's under outbreeding:

	Daughter	Son	Mother	Father	Sister	Brother	Nephew/ Niece
Female	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{3}{4}$	$\frac{1}{4}$	$\frac{3}{8}$
Male	1	0	1	0	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{4}$

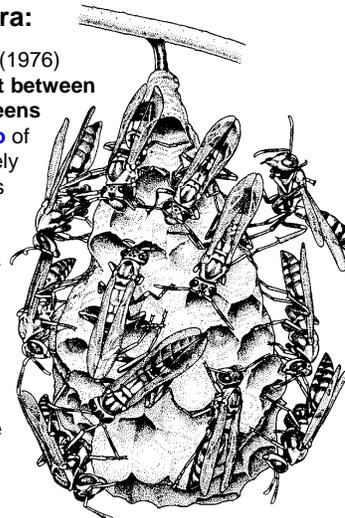
- Under monogamy, r is especially high between sisters ($\frac{3}{4}$) and especially low between sisters & their brothers ($\frac{1}{4}$).
- If females can add more sisters to the world, at the cost of their own offspring, they can **trade an r of $\frac{1}{2}$ for an r of $\frac{3}{4}$** (Hamilton 1964).
- And because they're less related to their brothers, they should raise relatively more sisters than brothers (3x as many) (Trivers & Hare 1976).
- This genetic system is *predisposed to evolving eusociality*.



Supporting data?

Hymenoptera:

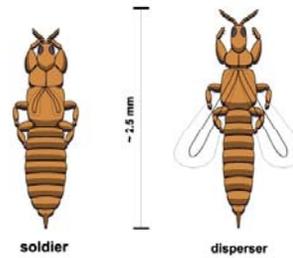
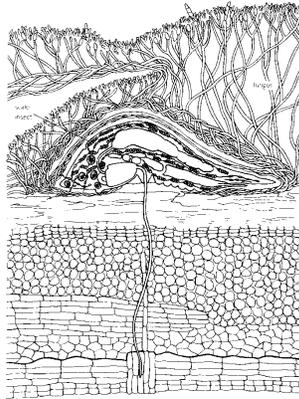
Trivers and Hare (1976) predicted **conflict between workers and queens** over the **sex ratio** of the colony – largely due to the various asymmetries of relatedness that result from haplo-diploidy.



1. Indeed, the sex ratio of colonies has been shown to vary according to prediction (Bourke & Franks 1995):
 - 3:1 in single-queen species, where workers control the sex ratio.
 - 1:1 in multiple-queen species or slave-making species, where relatedness of worker females is closer to $r = \frac{1}{2}$.
2. And there have been multiple, **independent eusocial origins** in Hymenoptera.

Has eusociality evolved **independently**
in haplodiploid taxa **unrelated** to Hymenoptera?

Altruistic female **scale insects** (Coccidae) are impregnated by a symbiotic fungus; the impregnated scale does not reproduce, but protects reproductives under the thicker fungal mat.

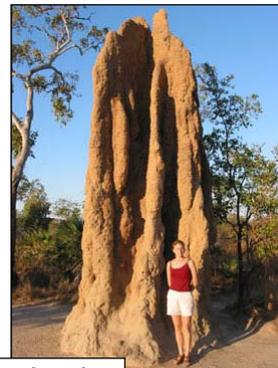


- Castes and herds have evolved in haplodiploid social units (herds) of thrips – order **Thysanoptera** (Crespi *et al.*)
- **Mites** (Acari) are also haplodiploid, and some show sociality.
- But **other eusocial clades are not haplodiploid** – e.g., termites, and naked mole rats.



Eusocial **diploid** clades: hypotheses?

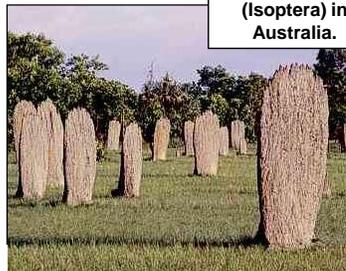
- There is no lack of hypotheses!
- Lately, emphasis has been on **ecological** explanations.
- **“Best of a bad job”** is now thought to be the driving force in, say, **eusocial termites**:
 - Nest building and care of larvae – as in the bee-eaters – all make it too difficult for the female to breed on her own.
 - Solution: Cooperative nest founding by several females; then turn your young into helpers.



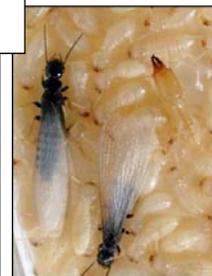
- Also true of eusocial **naked mole rats**:

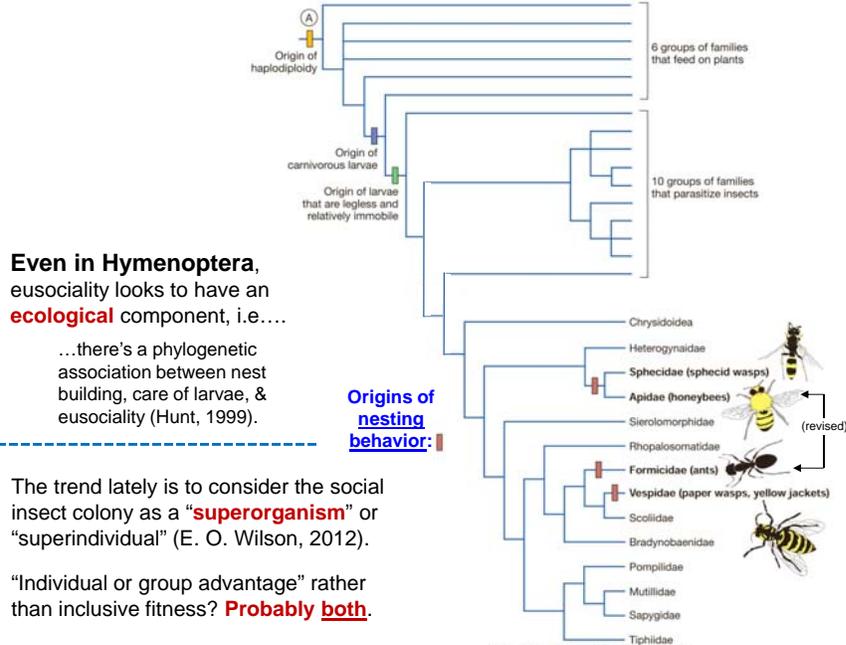


Heterocephalus glaber (E. Africa)



Nests of termites (Isoptera) in Australia.





Pairwise cooperation among **unrelated** individuals:
(1) **By-product Mutualism** (*individual advantage*)

- Individuals incur an *immediate cost* or penalty for not acting cooperatively – usually attributable to a **harsh environment**.
- So the immediate net benefit of cooperating outweighs cheating – largely because there's *no time lag* during which one could cheat.
- **Example 1:** Group hunting behavior in lions (Packer, 1991 etc.).
 - Lions cooperate when hunting big game...
 - but they hunt individually (selfishly) when going for smaller prey.



(Relevant studies by Grinnel et al 1995, Heinshohn & Packer 1995)

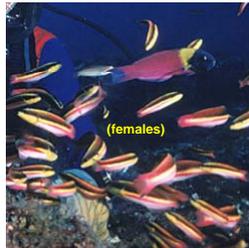
By-product mutualism, another example: **Fishes**

(Susan Foster 1987)

- The **rainbow wrasse**, *Thalassoma lucasanum*, feeds on embryos of sargent-major **damselfish**, *Abudefduf troschelli*.
- But the damselfish embryos are well protected by their nesting parents.
- In order to have any success at foraging, the wrasse need to **group** into schools.
 - Groups of 30 or less were never able to get access to the food.
 - Only groups of 100 or more experienced high foraging success.
 - And when the damselfish were *NOT* nesting, such large groups of wrasse were never seen.



Thalassoma lucasanum
(Rainbow wrasse, male;
probably used to be a female)



Pairwise cooperation among *unrelated* individuals:

(2) **Reciprocal Altruism** (Trivers 1971)

- Within a species, an individual “chooses” to act altruistically toward another who has already acted altruistically toward that individual.
- Selection will favor this type of interaction, if...
 1. the cost of the act to the actor is less than or equal to the benefit to the recipient, and...
 2. individuals that fail to reciprocate are punished in some way (otherwise “cheater” alleles would take over). E.g....
 - physical assaults
 - withholding future benefits

Other characteristics favoring the evolution of reciprocal altruism:

3. Groups are stable, so individuals *repeatedly interact*.
4. *Many opportunities* for altruism occur in a lifetime.
5. Individuals have *good memories* (which rules out most animals!)
6. Potential altruists interact in *symmetrical* situations.

As in by-product mutualism, **R.A. models cooperation in non-relatives.**

Reciprocal altruism and Game Theory

- This type of interaction is extremely vulnerable to cheating, because the *greatest attainable payoff goes to the recipient of a cooperative action who fails to reciprocate*.
- Game Theory is an *economic tool* initially developed in 1928 from games such as chess. It seems relevant to R.A.
- Practitioners have included John Maynard Smith (1974, 1982), R. L. Trivers (1971), W. D. Hamilton (1981), and R. Axelrod (1981, 1984).
- The **Prisoner's Dilemma**: Two suspects are interrogated separately by the police, and they know that...
 1. If both cooperate: each receives payoff **R** (reward).
 2. If someone cheats (defects), but the other cooperates: he/she receives **T** (temptation to cheat).
 3. If both cheat: each receives payoff **P** (punishment).
 4. The one who cooperated when his partner cheated: receives **S** (sucker's payoff).
- **You should cheat** if you only play once – but in **iterative re-matches**?

The “Iterative Prisoner's Dilemma”

Classic flavor (and hence the name):

	Prisoner B Stays Silent	Prisoner B Betrays
Prisoner A Stays Silent	Each serves 6 months (mutual cooperation)	Prisoner A: 10 years Prisoner B: goes free
Prisoner A Betrays	Prisoner A: goes free Prisoner B: 10 years	Each serves 5 years (mutual defection)

Payoff matrix:

	Cooperate (B)	Defect (B)
Cooperate (A)	3, 3 [= R] (fairly good)	0, 5 [= S] (very bad: sucker)
Defect (A)	5, 0 [= T] (very good)	1, 1 [= P] (fairly bad)

Since the game is **iterative**, a player can punish the partner for earlier decisions.

- **Reward system:** $T > R > P > S$, and $2R > T+S$ (e.g.: $5 > 3 > 1 > 0$, and $6 > 5$)
- **Why?** To level the playing field a bit for cooperators vs. cheaters.

Solutions to the Iterated Prisoner's Dilemma

Deterministic solutions (here we're looking for **ESS's** – “evolutionarily stable strategies,” which are strategies employed by a population of individuals that *cannot be invaded* by a rare mutant adopting a different strategy).

1. **Tit for Tat** (TFT): *Cooperate on the first encounter* with an opponent (because the previous move cannot be known) and, in subsequent encounters, *copy the opponent's last move*.
 - “niceness” – someone doing TFT is never the first to cheat.
 - “swift retaliation” – you immediately respond to cheating by cheating.
 - “forgiving” – you remember only 1 move back and therefore forgive prior defection by the currently cooperating opponent.
2. **Tit for 2 Tat** (TF2T): Requires *two consecutive defections* for a defection to be returned.
3. **Suspicious Tit for Tat** (STFT): *Always defect on the first move; then copy the opponent's last move*.
4. **Special**: a player with a “theory of mind”** can use extortion strategies to always win (Press & Dyson 2012).

** the capacity to understand that others have beliefs, desires, and intentions that are different from one's own.

Deterministic (ESS) vs. Stochastic solutions

- **Tit for Tat always wins**, even when the players know that it is going to win and should therefore be trying some alternative strategy.
- But other strategies do better than TFT under certain conditions.
- **TFT is an ESS...**
- But it is only an ESS with respect to the other strategies employed in the tournament (Axelrod & Hamilton 1981)

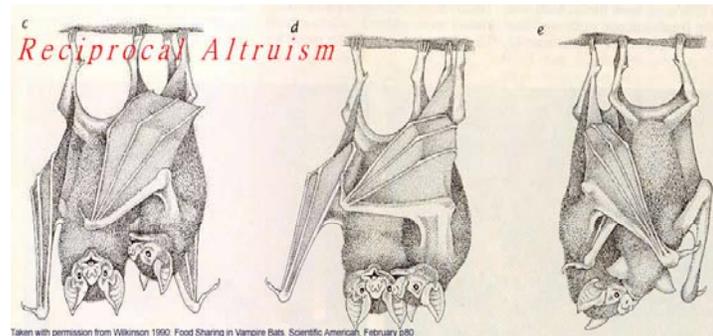
Assuming that TFT is *not* an ESS under all possible scenarios, ***stochastic** strategies are likely to perform better on a real-world stage

- There are just about *NO* examples of real organisms in nature solving the Prisoner's Dilemma by known strategies.
 - This is likely due to how hard it is to document (and remember) the moves by the players.
- Which brings us back to **reciprocal altruism** – which DOES seem to occur in nature, is easier to document, & often *approximates TFT*.

* **stochastic**: moves are probabilistic rather than mathematical, and are made in response to new random configurations at each iteration based on the previous state and the moves of the players.

Good candidates in nature for reciprocal altruism

- Individuals should have long lifespans (many opportunities for altruism).
- Colonies should have low dispersal rates (groups are stable).
- There should be no significant asymmetries in the relationship between individuals – e.g., such as those caused by a strong dominance hierarchy.

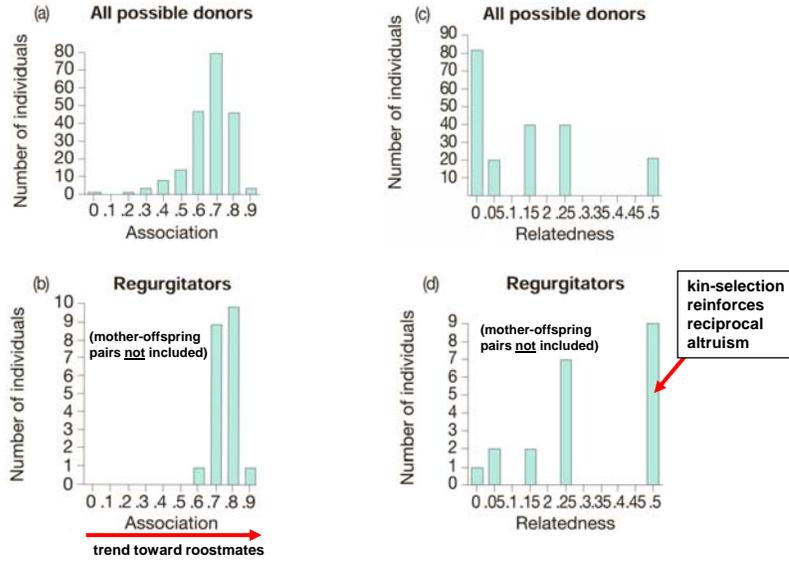


Wilkinson demonstrated:

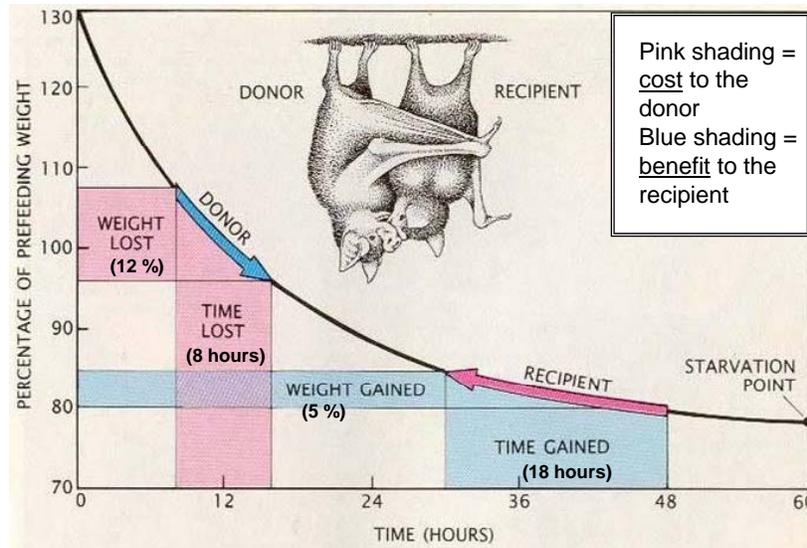
- Individual females associate for long periods of time.
- The degree of association predicts the degree of altruism, *independently* of kinship (although the latter does have an effect).
- Benefits are larger than the costs.
- Roles of donors and recipients frequently reverse.
- Individuals are most likely to aid those individuals that have recently helped them.

Vampire bats (Wilkinson 1984)

Regurgitators are more likely to be related and more likely to be roostmates than the general population.



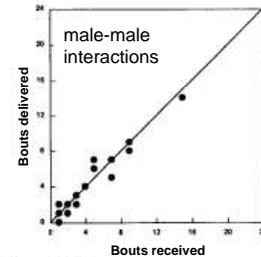
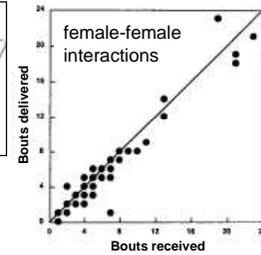
Wilkinson 1990 (*Scientific American*)



Another likely example of reciprocal altruism:
the Impala, *Aepyceros melampus* (Hart & Hart 1992)



- Type of exchange = reciprocal **allo-grooming**.
- Occurs in short bouts, which are almost always symmetrical. Is $B > C$?
- **Costs** = energy, salt loss, tooth wear, some decrease in vigilance (but there *are* two of them).
- **Benefit** = parasite removal (less blood loss, less disease). It is likely that $B > C$ prevails.



Cooperation between non-relatives via Manipulation

- Here, individuals are not simply non-relatives; they may belong to different species...
- e.g., parasitism may trigger what looks like altruistic behavior.
- The recipient **induces altruism** that would normally be directed elsewhere, or not at all.
- *Examples: Brood parasites in birds.*

- **Conspecific brood parasitism:** American coot will lay eggs in conspecific nests.
- Hosts can count eggs (8), and also recognize their own eggs (speckling pattern)
- 43% rejected one or more parasitic eggs (Lyon 2003).
- Though it's OK to incur costs on behalf of kin, avoid paying costs on behalf of non-kin!



Altruistic hosts and their brood parasites

- **Interspecific brood parasitism** exists in cowbirds, cuckoos, and many other birds.
- In these interspecific interactions, selection has favored counter-adaptations on each side.
 1. **Host:** Tosses out odd-looking eggs.
 2. **Parasite:** Egg mimicry evolves.
 3. **Host:** Evolves the ability to count eggs.
 4. **Parasite:** Throws out one of the host's eggs so the count is right.
- This is *antagonistic co-evolution*, called **escalation** by Vermeij (1987).
 - Other **parasite** adaptations: early hatching, more rapid growth via aggression, throat-color matching, & similar vocalizations.
 - Other **host** adaptations: crushing the parasite to death in the nest.
- The secret for the parasite is to **pretend a degree of relationship to the host** that it doesn't actually possess.



II. The Origin and Maintenance of Sex

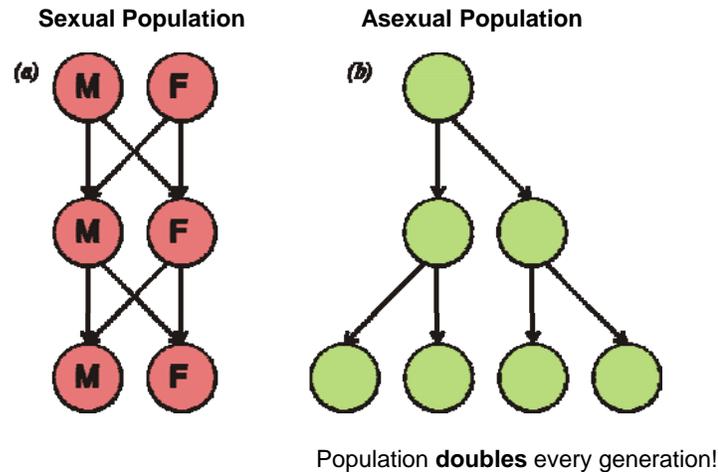
- Earlier, we covered *levels of selection, group selection, cost versus benefit, and conflict*.
- **All** have been invoked to explain **Sex** – “the outstanding puzzle in evolutionary biology” (G. C. Williams)
- In **sexual** reproduction, two gametes fuse to form a new organism. $\frac{1}{2}$ of all parental investment is spent on males, who don't (usually) make any parental investment in the young beyond their genes.
- In **asexual** reproduction, the female's gametes develop directly into daughters: there's no male contribution. All grow up to invest.
- So, **sex is expensive**. **Maynard Smith** (1971) first pointed out the **two-fold cost of sex**, relative to asexual reproduction (but see recent reviews →).
- An **asexual mutant** appearing in a sexual population should begin to double in frequency, and in 50 generations or so the entire species should be asexual.



The Two-fold Cost of Sex

(but see recent reviews: Lehtoin et al. 2012; Meirmans et al. 2012)

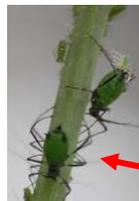
If each individual were to contribute to the same number of offspring (two):



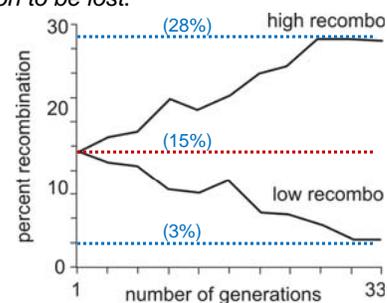
Sexual Reproduction

- In view of its huge apparent disadvantage, why does sexual reproduction predominate in plants and animals?
- Pre-existing bias? Some genetic or mechanical constraint, preventing loss of sex? – **NO**.

- It's easy enough to *substitute mitosis* for meiosis – the cellular machinery is all in place.
- It's easy enough for *gamete fusion to be lost*.
- And the process of loss of sex is abundantly documented by experiment, w/ lots of genetic variation for recombination rate and mode of reproduction.



1. % recombination in  *Drosophila*.
2. frequency of self-fertilization shows wide range of *natural* variation.
3. parthenogenesis & sex often **co-occur** in one species.



Sexual reproduction must therefore be **adaptive**

For sex to be adaptive, each sexual female must produce a daughter who will be *twice as fit* as a simple copy of herself.

Two sets of explanations: group selectionist, and individual selectionist.

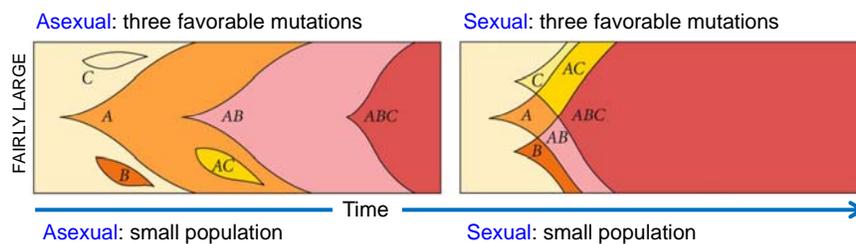
Explanations invoking group selection:

1. More rapid evolutionary change and adaptation (Fisher 1930)
2. Resisting deleterious mutation accumulation (Müller 1930)
3. Lineage selection favoring sexual taxa (Nunney 1989, 1999; de Vienne et al. 2014)

Explanations invoking individual selection:

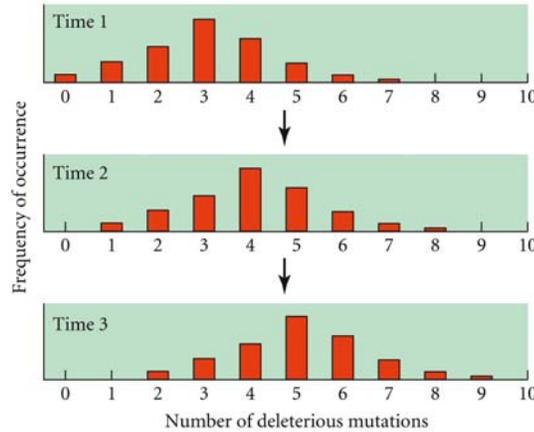
1. Genetic variation among siblings.
 - a. The basic hypothesis is Weismann's (1889)
 - b. Sibling competition (G. C. Williams 1975)
 - c. The "tangled bank" (Ghiselin 1974)
2. Environmental variability models (Red Queen: van Valen 1973 etc.).
 - a. Unpredictable (but predictably changeable) biotic environment.
 - b. ...especially, Host-parasite co-evolution (Lively, many papers).

Group selection: 1. "**Rate of evolution**" model (Fisher 1930)



- Assume that **A**, **B**, and **C** are new, **advantageous** mutations.
- In fairly large **asexual** clones, advantageous mutations must appear successively in a genealogical line, because single individuals with more than one such mutation will be vanishingly rare.
- In fairly large **sexual** populations, **A** and **B** arise in different individuals but are soon combined in a single individual without having to wait for the mutation to occur twice.
- **Recombination** speeds up the appearance of individuals with more than one favorable mutation, thus favoring sexual populations.

Group selection: 2. **“Mutation accumulation” models** --
Müller’s Ratchet (1932) and “Müller’s Hatchet” (Kondrashov 1993)



Asexual clone: Deleterious mutations will appear over time, and can be eliminated only by back mutation (the **Ratchet**).

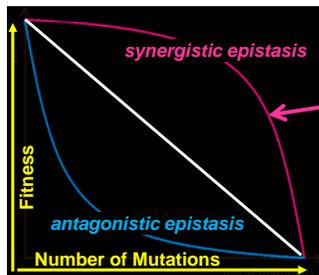
Sexual line: Recombination will continuously produce some individuals *largely free of negative mutations* (the **Hatchet**).

So sexual reproduction acts like a hatchet and broom, **sweeping** the population clean of deleterious mutations.

Especially high impact on **males** (fitness genes on X-chromosome – Mallet et al. 2011).
[**Note:** 100x too slow in *Caenorhabditis* to give an advantage to sex – Artieri et al. 2008]

Kondrashov’s hatchet (1988, 1993): Details & assumptions

Ex.: Escaping $Aa^x \times Aa^x$
Müller’s ratchet: 1: 2: 1
 $AA \quad Aa^x \quad a^x a^x$
(25% zero mutants through recombination)

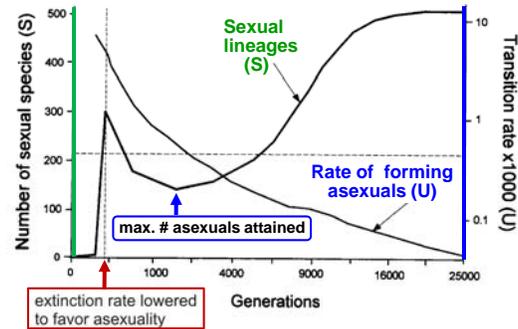


- The majority of deleterious mutations are only slightly harmful.
- But the introduction of each additional mutation has an increasingly large effect on fitness (red curve).
- Most of the population will consist of individuals with **few** harmful mutations.
- Sex acts to recombine these genotypes, creating individuals with **several** deleterious mutations.
- Each genetic death can thereby eliminate *more than one* deleterious mutation.

• Requires a deleterious mutation rate of >one/genome/generation.
• **Synergistic** epistasis seems no more likely than additive or antagonistic epistasis.

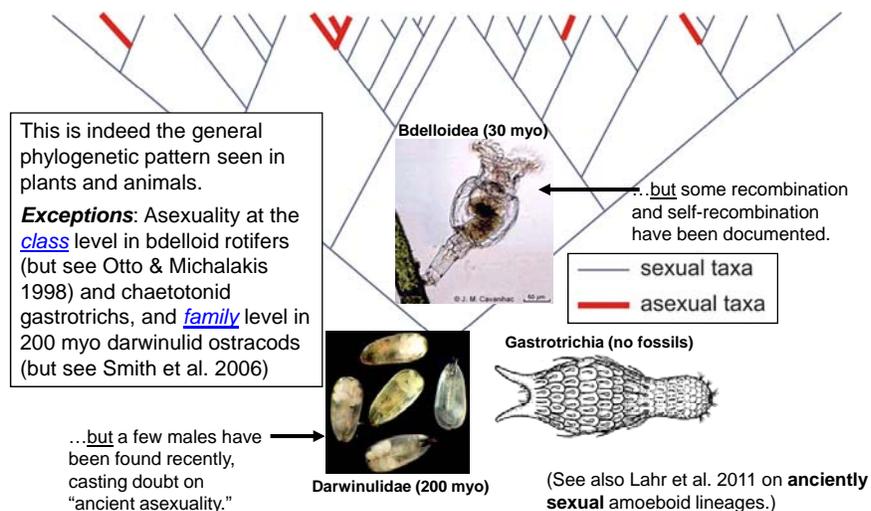
Note: Desai et al (2007) show **antagonistic epistasis** is **more** likely...

Group selection: 3. **“Lineage selection” models** (Nunney 1989, 1999)



- **Sexual lineages (S)** prone to give rise to asexuals do so, and strong **short-term** selection causes the rapid transition of these lineages to asexuality.
- But the resulting parthenogenetic species have a relatively **high extinction rate**, so these lineages disappear over the **long term**.
- The remaining species are primarily those that **retained sex**: retention is a direct consequence of their declining rate (**U**) of forming asexuals.
- Sex is retained because the species that persevere lack the opportunity to become parthenogenetic.

Predicted phylogenetic pattern if these group-selection scenarios are correct: Spindly distribution of exclusively **young** asexual taxa



Examples of young asexually-reproducing taxa

Apomictic dandelions: Recently evolved asexually-reproducing composites that retain all the pollinator-attraction features of their sexually-reproducing ancestors.



Taraxacum officinale



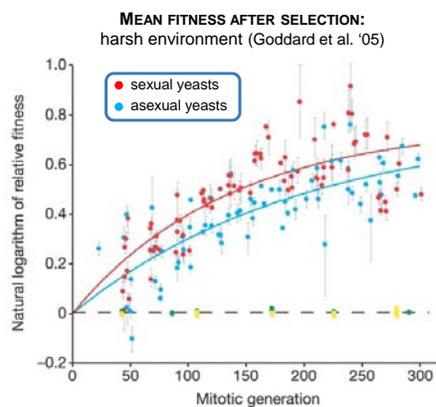
Individual selection:

1. Genetic variation among siblings

A. Weismann (1889) first suggested that the advantage of sex is the creation of *variation among siblings*.

- This does not function to increase mean fitness (\bar{w}) directly...
- Instead, it increases the **variance of fitness** – and thus the response to selection (R), and the mean fitness *after selection*.
- That is, individuals that reproduce sexually have progeny that are more variable, and so subsequent descendants are more fit (Burt 2000).

(Recent support:
Aguirre & Marshall,
2012, on ascidians)
[= tunicates]



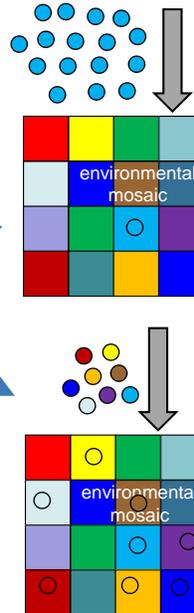
Individual selection: 1, continued.
Genetic variation among siblings

B. G. C. Williams (1975) turned this idea into a *sib-competition* (verbal) *model*.



G. C. Williams

- Imagine some patches that can ultimately support only one individual, but into which many offspring settle.
- **Asexuality** introduces into each patch **redundant** chances of success.
- But each offspring of a **sexual** parent represents a **unique** chance.
- **Analogy: Is it better to hold several tickets to a lottery with all the same number, or only half as many tickets but each with a different number?**
- Where siblings are thrown into competition and selection is intense, sex has a net advantage.



Individual selection: 1, continued.
Genetic variation among siblings

C. The “*Tangled Bank*” hypothesis (Ghiselin 1974)

- Named for the famous passage from Darwin (1859), “It is interesting to contemplate an entangled bank, clothed with many plants of many kinds, with birds singing on the bushes...”
- Argues that a *diverse set of siblings* may be able to extract more food from its environment than a clone, because each sibling uses a slightly different niche – *sib competition is reduced by differences among sibs*.

Problems with all sib-competition models (Cartwright 2000):

Sex should be most favored in *short-lived* organisms with *lots of small offspring* who compete with one another...

1. yet “lots of small offspring” is more prevalent in asexually-reproducing taxa.
2. And dispersal should allow escape from incompatible patches.



Individual selection: 2.
Environmental Variability

(van Valen 1973; Becks & Agrawal 2013; Green & Mason 2013; Griffiths & Bonser 2013; Park et al. 2014)

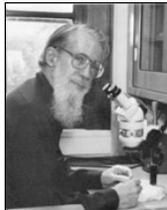
The “Red Queen” of
Lewis Carroll (1871)

“Well, in our country,” said Alice, still panting a little, “you’d generally get to somewhere else — if you ran very fast for a long time, as we’ve been doing.”

“A slow sort of country!” said the Queen. “Now, here, you see, *it takes all the running you can do, to keep in the same place*. If you want to get somewhere else, you must run at least twice as fast as that!”



Lewis Carroll's
*Through the Looking Glass, and
What Alice Found There*
(illus. by John Tenniel)



Individual selection: 2.
**Environmental
Variability, continued**

The “Red Queen” of Van Valen, 1973:

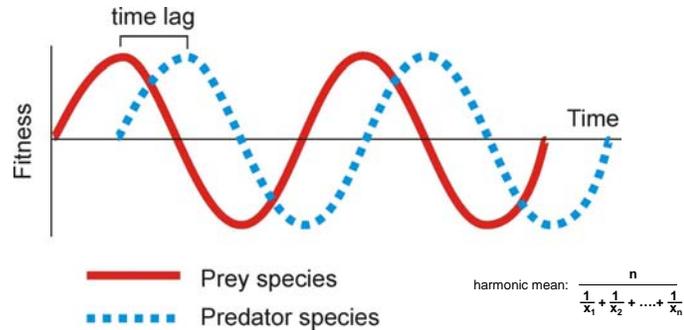
Over time, the environment is always deteriorating for each species, such that each must evolve (run) in order to maintain fitness relative to other species (to stay in one place)

- Temporal environmental variation only favors sex when **successive states are negatively correlated in time**: i.e., the environment is “contrary,” reversing every generation or two.
- The **physical** environment is an unlikely candidate for this, since it usually shows reasonably **positive** correlations or **trends** over time.
- But the **biotic** environment **is contrary** – note **antagonistic pairs** such as predator & prey, competitor & competitor, or parasite & host.



Lewis Carroll's Red Queen
(with Alice)

Antagonistic co-evolution: Fitness fluctuations of a prey (host) genotype with a predator (parasite) genotype (Hamilton 1980; et al. 1981)

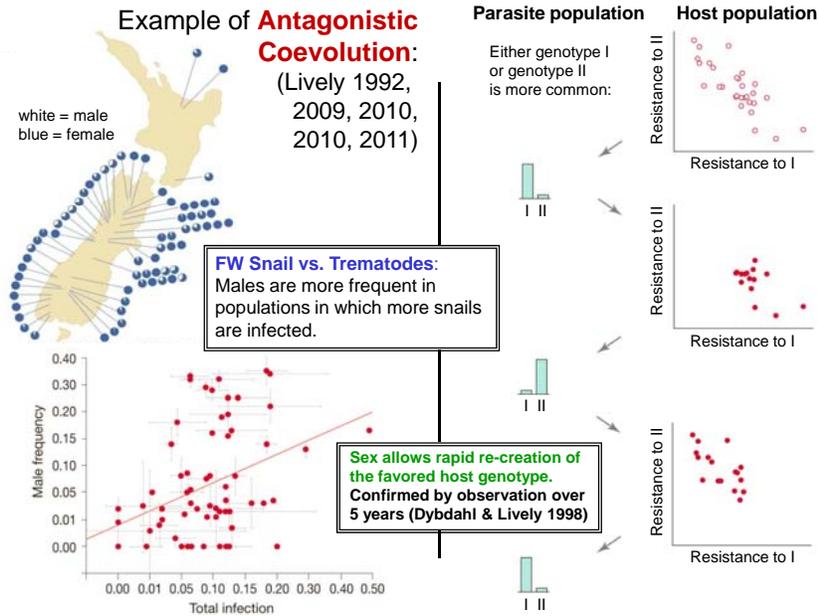


- Simple mechanism: *frequency-dependent selection* leading to frequency dependent fitness.
- The *quicker* the cycle, the greater the immediate benefit of sex.
- Also: the fitness cycles for sex genes will have **lower amplitude** than those of the genes for asexual reproduction.
- Lower amplitude = **higher harmonic mean of fitness for sexuals**.

More tidbits:

- In an asexual population of hosts, offspring will only have the different parasitic resistance if a mutation arises.
- In a sexual population of hosts, however, offspring will have a new combination of parasitic resistance alleles.
- Alleles of “future usefulness” remain in the sexual population longer, **available to re-generate genotypes that had been useful in the recent past**.
- Sexual species are “guilds of genotypes committed to free fair exchange of biochemical technology for parasite exclusion.” (Hamilton 1981)





Characteristics of species that tend to be sexual vs. asexual generally **conform to predictions** of antagonistic co-evolution

Sexual Species	Asexual Species
Marine	Fresh water
Large bodies of fresh water	Small bodies of fresh water
More distant from shore in the ocean	Closer to shore in the ocean
Large organisms	Small organisms
Low latitudes	High latitudes
Low altitudes	High altitudes
Wet	Dry
Undisturbed	Disturbed
Productive	Unproductive
Parasitic	Free-living

Asexual reproduction predominates in novel, disturbed habitats with low intensity of interspecific interactions.

Note: Support from a recent model of Scheu & Drossel, 2007

**So why is sex maintained despite the
(oversimplified) two-fold advantage of
asexual reproduction?**

There's probably no single reason, but the **combination** of factors conspire to make sexual reproduction highly adaptive (the [Pluralistic View](#) – see Meirmans & Strand, 2010).

