## ***Species*** or ***Lineage*** *level*

Levels (of organization) ***above*** that of the individual organism:

higher levels

- **lineage** – multiple species from a common ancestor (clade)
- **species** (sometimes called a lineage)
- population – race, ecotype
- trait group – packs, schools, other cooperative social units
- kin group – immediate and extended families

Levels ***below*** that of the **individual organism**:

lower levels

- tissue/organ – (unlikely)
- cell line – cancers
- organelle – mitochondria, chloroplasts, endosymbionts
- chromosome – X and Y sex chromosomes vs. autosomes
- gene (cistron) – segregation distorters, outlaw alleles

## ***Species*** & ***lineage*** **selection**

**Group selection can have *evolutionary consequences***, even if it *never* over-rides individual selection.

1. Individual selection could lead to the establishment of different adaptations in different groups:
    - *Example*: large body size in a clade of organisms might be…
        - favored by individual selection (defense, fecundity, etc.), but
        - disfavored by group selection (consumption of limited resources).
    - Long-term consequence: body size decreases over evolutionary time.
2. Those different adaptations result in different rates of ***group extinction*** or group expansion (***reproduction***).
    - The kinds of groups that become extinct less often will increase in frequency…(lower "***d***")
    - …as also will the kinds of groups that multiply faster (higher "***b***").
    - Evolutionary innovations and empty niches obviously influence this process.
3. Implication: that the species or lineage can have the property of **individuality**.

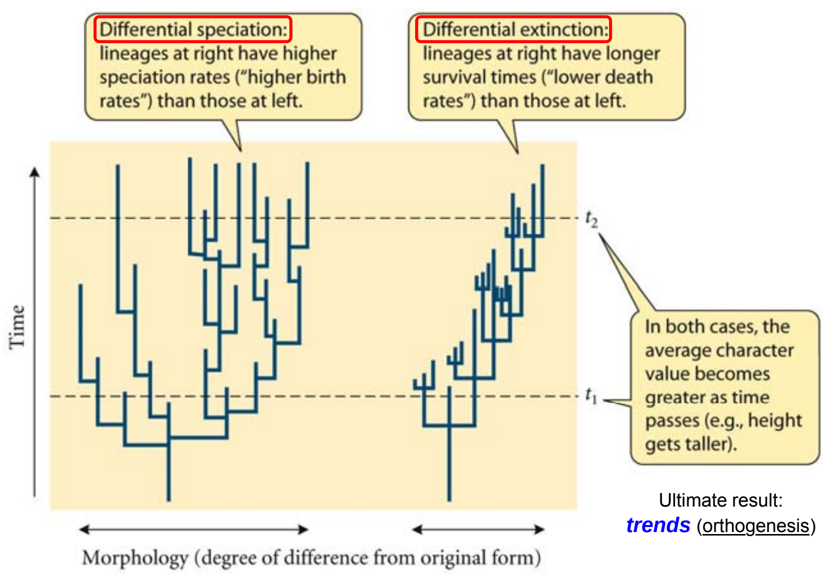
Contributors: Stanley 1975; Van Valen 1975, 1976; Gould (w/Lloyd) 1998-2000.
Recent reviews: Jablonski 2008; Raboski & McCune 2010; Pennell et al. 2014).

## **Species selection** & **lineage selection**

Species/lineage selection probably does requires that the species or lineage have the property of ***individuality***. Is this a problem?

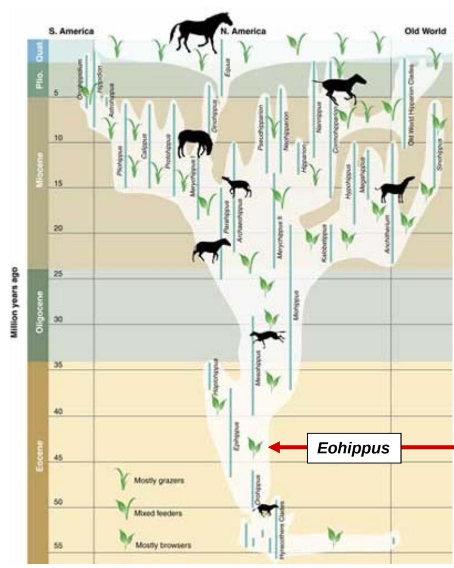
1. To be considered an individual, the species/lineage must possess or show:
   - variation [among species] in traits that are ***heritable;***
   - variation in traits that influence the probability the species will…
     - ***survive*** [avoid extinction], and…
     - ***reproduce*** [speciate];
   - reasonable ***continuity*** [stasis] over time.
2. From this perspective, species DO have some properties of ***interactors*** and ***replicators***, because
   - species reliably pass on some structure or information to their descendants.
   - these inherited structures influence the "phenotype" of species.
   - species persist in a condition of stasis for reasonably long time intervals.
3. But their status as ***either*** is uncertain. Controversial and philosophical…

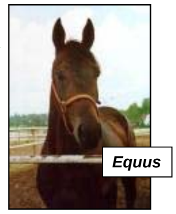
## **Group selection at the level of species and lineages** (Stanley)




Ultimate result:
***trends*** (orthogenesis)

**The effect of lineage selection on horse evolution** (Benton & Harper 1997)




**"Orthogenesis"**
**-- larger body size**
**-- longer legs**
**-- longer teeth**
**-- fewer toes**

## *Kin-group level*

Levels (of organization) ***above*** that of the individual organism:

higher levels

- lineage – multiple species from a common ancestor (clade)
- species (sometimes called a lineage)
- population – race, ecotype
- trait group – packs, schools, other cooperative social units
- **kin group** – immediate and extended families

Levels ***below*** that of the **individual organism**:

lower levels

- tissue/organ – (unlikely)
- cell line – cancers
- organelle – mitochondria, chloroplasts, endosymbionts
- chromosome – X and Y sex chromosomes vs. autosomes
- gene (cistron) – segregation distorters, outlaw alleles

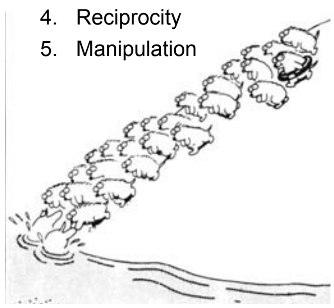
## **Kin-group selection** and ***inclusive fitness***

- "**Kin group**" – a special type of group that contains closely related individuals.
- In a different way than species-level selection, kin-group selection eliminates conflict between group-level and organism-level selection.
- If group members are kin, then you are favoring your own genes (fractionally), and therefore yourself, when you help them.
- Your actions can enhance your individual fitness, even though they are directed toward your relatives in the group at some direct cost to you.
- So: *Your fitness is the sum of your own direct fitness plus some proportion of the fitness you confer on genes that you share with your relatives by direct descent, minus the cost of your unselfish actions*.
- This is ***inclusive fitness***, formalized in a series of key papers by William D. Hamilton in 1963 and 1964.
- They show how group fitness can be translated into individual fitness.

The basic problem addressed by this concept is **altruism** – itself a part of ***cooperative behavior***.

## **Cooperation and Altruism**

- An ***altruistic trait*** is a trait (or an act) that confers a ***benefit*** on someone else at a ***cost*** to the actor.
- Costs & benefits are in units of reproductive success (fitness).
- Cooperation, which includes altruism, is a basic ingredient of social interactions, social behavior, and societies.
- There are different evolutionary paths to cooperation:
    1. Group selection (earlier).
    2. By-product mutualism
    3. **Kin-selected cooperation**
    4. Reciprocity
    5. Manipulation



## Cooperation due to kin-group selection and inclusive fitness

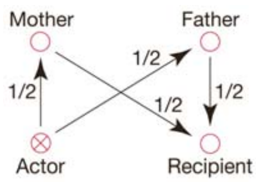
- Kinship is based on the ***degree of relatedness*** (***r***) of individuals in a group.
- Measures of inclusive fitness show that apparent sacrifice by the "actor" may be genetically self-serving.
- Darwin first recognized greater cooperation among relatives (1859).
  - Haldane re-discovered cooperation among relatives in 1932…
  - …and codified it in his1955 "drowning man" example (later).
- Degree of relatedness, ***r***, measures the percentage of genes that are identical by descent (IBD) between two individuals (Sewall Wright 1948).
- In diploid, 2-parent organisms, each individual gets half its genes from each parent (on average):

$r_{\text{parent-offspring}} = 0.50$ This is a *symmetrical* relationship.

We use ***r*** to ***weight the benefit*** to the recipient of an altruistic act, compared to the ***cost paid*** by the altruist (the actor) – i.e., is it worth it to be altruistic?

Costs and benefits are measured as ***reproductive success*** (fitness).

### Full-siblings

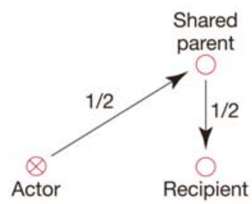



Actor to recipient via mother:
$r = \frac{1}{2} \times \frac{1}{2} = \frac{1}{4}$

Actor to recipient via father:
$r = \frac{1}{2} \times \frac{1}{2} = \frac{1}{4}$

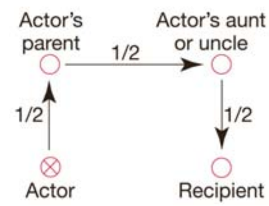
Actor to recipient, sum:
$r = \frac{1}{4} + \frac{1}{4} = \frac{1}{2}$

### Half-siblings




Actor to recipient via shared parent:
$r = \frac{1}{2} \times \frac{1}{2} = \frac{1}{4}$

### Cousins




$r = \frac{1}{2} \times \frac{1}{2} \times \frac{1}{2} = \frac{1}{8}$

## Relatedness calculations

**Reminder:**

- The probability of two events happening *simultaneously* is the ***product*** of the two independent probabilities.
- The probability of an event that can happen *in two or more ways* is the ***sum*** of the independent probabilities.
- So, tracing the genealogical connections from one individual to another, we ***multiply*** the ***r***'s that connect the various individuals, and if 2 individuals are related through more than one genealogical connection, we ***add*** the values for each connection.

## Hamilton's Rule (1964)

An altruistic gene enjoys a *NET* benefit when the benefit to the recipient weighted by the degree of relationship of the altruist ('actor') to the recipient is greater than the cost suffered by the altruist:

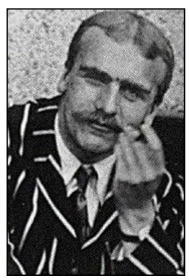
**B*r* > C**, or B*r* – C > 0 (***r*** can range from 0 to 1)
(Hamilton's Rule)

Note from this that as ***r*** gets smaller, the benefit must get proportionately larger to compensate for a given cost to the altruist.

So before you will consider helping your **half-sib** ($r = \frac{1}{4}$), the benefit to him/her must be four times the cost to you, e.g.,

$$(B/4) - C > 0, \text{ or } (B/4) > C, \text{ or } \mathbf{B > 4C}$$

## Haldane's insights prior to Hamilton's Rule

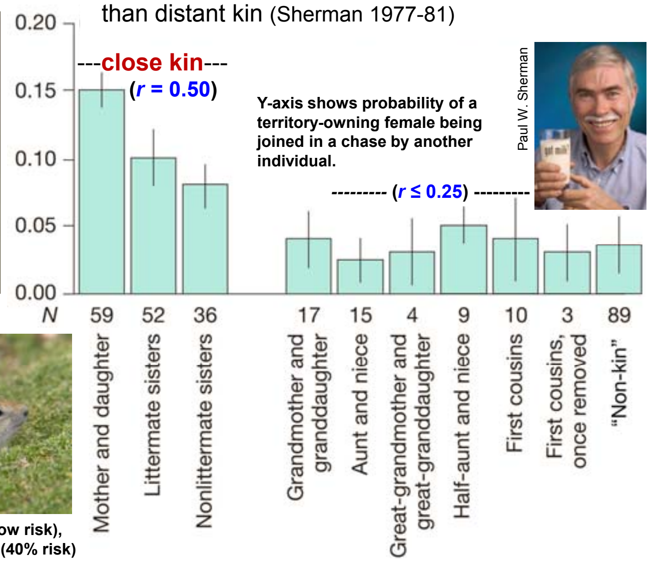


- Way before Hamilton, in 1955, J. B. S. Haldane nearly came up with "Hamilton's Rule."
- When once asked if he would risk his life to save a drowning man, Haldane replied, *"No. But I would to save two brothers or eight cousins."*
  - Oddly, he hobbled the general principle because of a personal experience, where he jumped right in without considering relatedness.
  - He therefore concluded that his impulse would be true for all creatures, so he used an average degree of relatedness within social groups of **<< $^1/_{10}$**, making the concept of kin selection irrelevant.

❖ On the danger of a perforated eardrum from his personal decompression chamber experiments: "The drum generally heals up; and if a hole remains in it, although one is somewhat deaf, one can blow tobacco smoke out of the ear in question, which is a social accomplishment."

**Evidence** for kin selection? Closely related **female Belding's ground squirrels** (California) are more likely to cooperate than distant kin (Sherman 1977-81)

*Spermophilus beldingi*




Note: whistles to raptors (low risk), complex trills to mammals (40% risk)

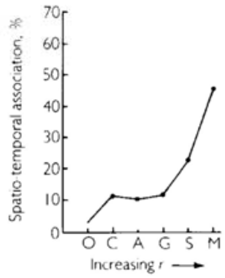
More evidence: Grooming and helping among relatives in **Japanese macaques** (Jeffrey A. Kurland 1977)

- As ***r*** increases, monkeys spend a greater percent of time near each other (proximity)
- After correcting for proximity, the monkeys directed altruistic acts preferentially toward *closely related* individuals.
- They reserve selfish acts for distant relatives.

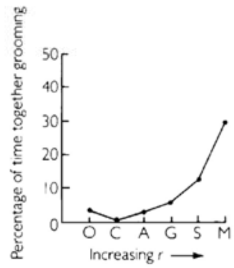
- ***Alloparenting***: Is it *altruistic* (saves the mother work and time) or *selfish* (at a cost to the offspring)?
- Alloparenting was most common in females who hadn't yet given birth, and was directed at unrelated individuals.
- Conclusion: alloparenting is usually selfish, preparing the young female to be a better mother.

## **The data** (Kurland 1977)

Spatial proximity as a function of kinship




Frequency of grooming as a function of relatedness (corrected for proximity)

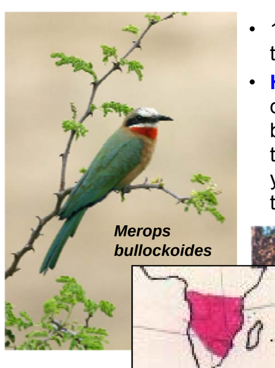



Kinship categories among Japanese monkeys:

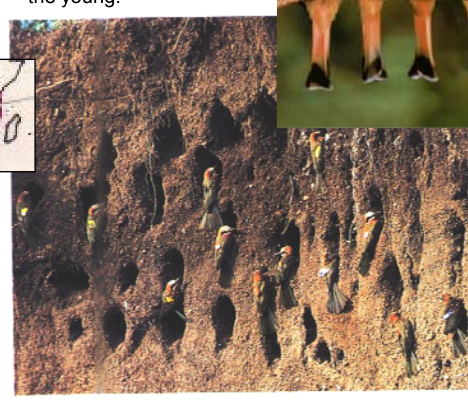
**0.50** M = mother-offspring
**0.50** S = siblings
**0.25** G = grandmother-grandoffspring
**0.25** A = aunts-nephews/nieces
**0.125** C = cousins
**< 0.125** O = other matrilines

## Kin-selection in **white-fronted bee-eaters**, *Merops bullockoides*

(papers by Emlen, Wrege, & Demong from 1982-1995)

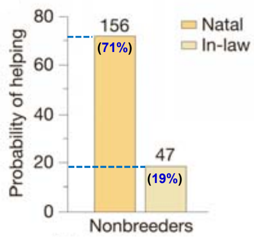


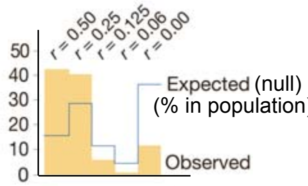

- 15–25 families roost together.
- **Helpers** *really help*: they dig nests, bring food to the brooding female, incubate the clutch, defend the young, and provide food to the young.



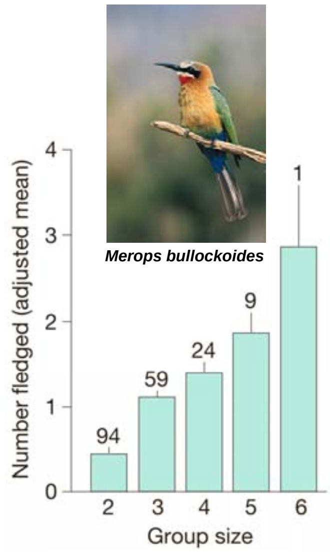
**Is helping behavior maintained through kin-selection?**

**Helpers (usually males) assist close relatives, and the help they provide is measurable**

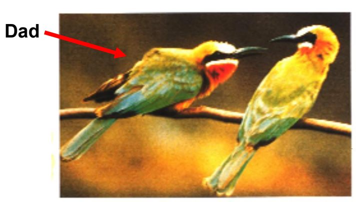


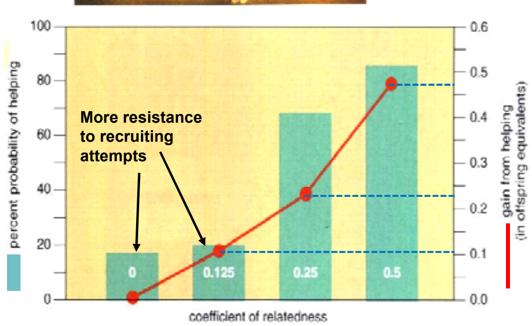

- **"Best of a bad job" situation: breeding opportunities are extremely restricted.**
- **On average, the nesting bird could raise an additional 0.47 offspring per helper.**




**Males recruit helpers by harassment, particularly of their own sons**



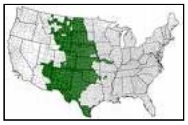

- Fathers coerce sons (close kin) into helping raise their siblings – they chase them off territories, disrupt courtship, harass them at their nests.
- Why? Sons are equally related to their own offspring and to their full sibs ($r$ = ½ ).



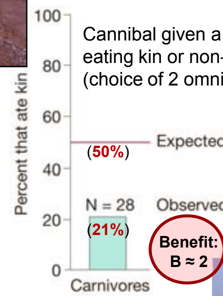

- Parents are closer to their own offspring ($r$ = ½ ) than to their grandchildren ($r$ = ¼ ).
- **Parent gains 0.47 offspring** from a helper son, which is almost the same (0.51) that it can raise by itself.
- So it's almost a toss-up, with close enough payoffs that parents can change *"the bottom line of fitness accounting."*

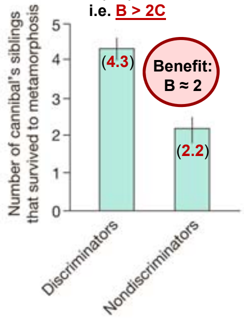
e.g., B$r$ – C > 0, $r$ = ½; then **B > 2C**, achievable by doubling # of fledged offspring

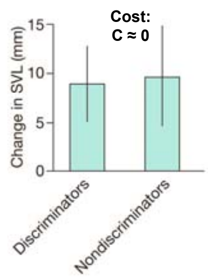
Cost-benefit analysis of kin-selected discrimination in **cannibalistic *spadefoot toad*** and ***tiger salamander*** larvae (Pfennig 1999)

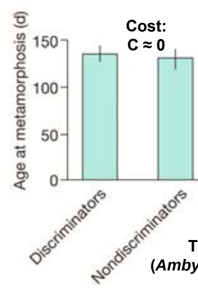


Avoidance of sibling cannibalism will be favored when B(1/2) – C > 0, i.e. B > 2C

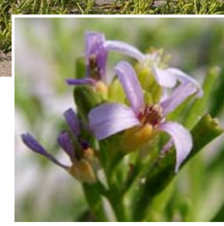



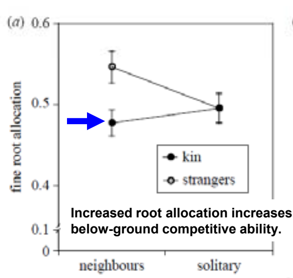



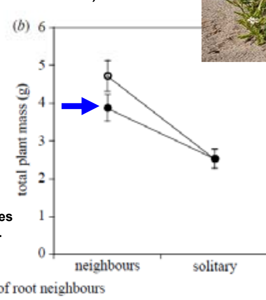




Tiger salamander (*Ambystoma tigrinum*)

**Cooperation & altruism in plants: less competitive phenotypes.**
***Cakile edentula*** (an annual), the Great Lakes Sea Rocket
(Susan Dudley & A. L. File 2007 )





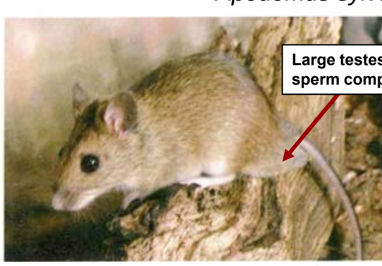

- Also shown in ***Impatiens pallida*** → (Murphy & Dudley 2009
- ← and ***Ipomea hederacea*** (Biernaskie 2011).
- And increased strength of **induced resistance in ramets** that receive herbivore-induced volatiles in sagebrush (Ishizaki et al. 2011)

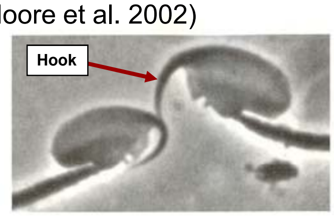
## Kin recognition and assessment of relatedness

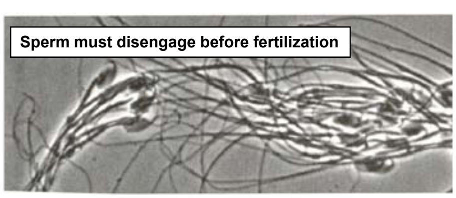
| "all good kumrads you can tell / by their altruistic smell" (e e cummings, 1930's) |
|---|

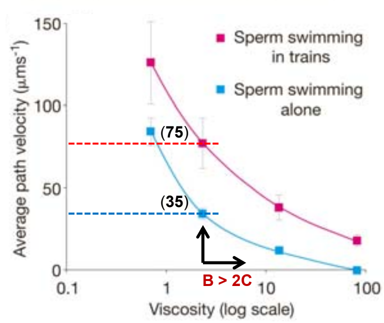
- From kin selection and inclusive fitness theory: Organisms will evolve to *recognize categories of relatives* – to measure the degrees of relationship.
- Animals may literally be able to *smell* kinship:
  - sweat bees checking out admittance to the hive.
  - water-borne chemicals mediating the sparing of kin by cannibalistic spade-footed toads and tiger salamanders.
  - MHC-mediated recognition and mate choice by mice, humans, & other mammals.
- Also involved may be early *spatial proximity* of individuals:
  - imprinting, or..
  - *phenotypic matching*, e.g., golden hamsters (Heth et al. 1998): the ability to measure one's own phenotype and compare it to others.
- Should a gene that directly recognizes itself in other individuals be considered an **outlaw gene**? Probably – see Gardner & West (2010) on **greenbeards**.
- Most likely: ***Learning*** at an early critical period to associate with individuals who are similar but not identical to themselves (i.e. imprinting; Bateson 1994).
- ***Plants*** can recognize kin, too (Lepik et al. 2012) – presumably chemically.

## **Altruistic sperm** that self-sacrifice in the European wood mouse, *Apodemus sylvaticus* (Moore et al. 2002)



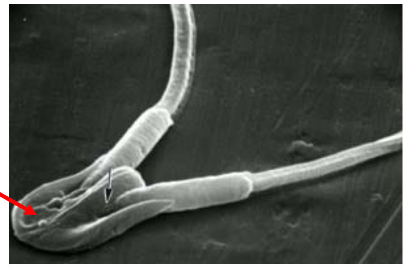




There should be conflict here, because ***r* = ½** among individual sperm. But B = *twice the cost?*

## **Cooperating sperm** in South American didelphid opossums (Moore & Taggart 1995; Sheffield & Taggart 1995)

headpiece

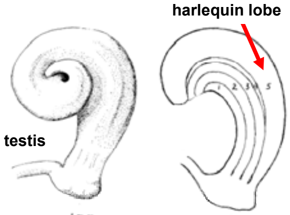



- 80% of the ejaculated sperm are joined together in pairs by headpieces.
- When paired, they can swim in a straight line in the extremely viscous environment of the female genital tract.
- When not paired, they swim in circles.
- They un-pair when they reach the egg, and one of them fertilizes it.
- In this example, as in the previous one, the ***benefits of cooperation*** are very high, and undoubtedly *greater than twice the cost*.

## Other adaptations involving **"helper sperm"**

**-- though top-down control can minimize potential conflicts.**

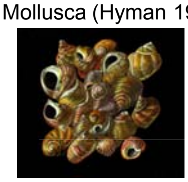
Hemiptera: Pentatomidae

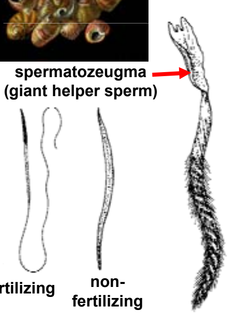



• Harlequin lobes in testes of stink bugs produce **giant helper sperm** (Shrader 1960).

• These helper sperm are akin to the apyrene (vs. eupyrene) sperm in Lepidoptera, which aid in **sperm competition** with sperm from unrelated individuals (Silberglied *et al*. 1984)

Mollusca (Hyman 1967)



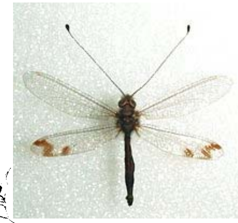


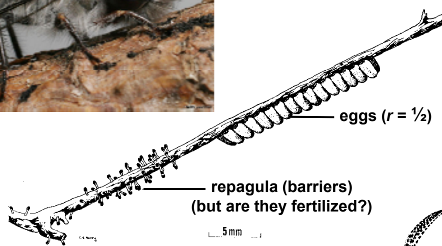

• Prosobranch molluscs have two types of sperm; non-fertilizing ones are digested.

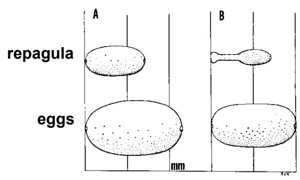
• Spermatozeugma is a huge helper sperm that carries hundreds of fertilizing sperm.

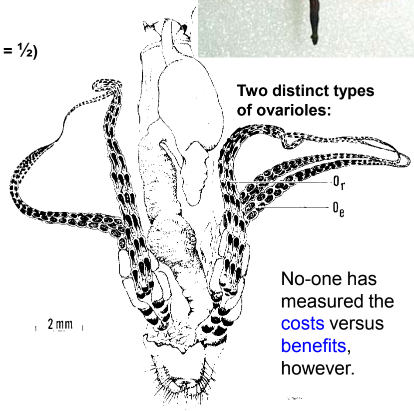
Helper eggs: **Egg altruism** in an owlfly, Ascalaphidae

(Neotropical *Ululodes* spp)






No-one has measured the costs versus benefits, however.

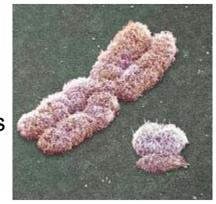
**Kinship and conflict** at the ***chromosome*** **level**

Degrees of relatedness of chromosome classes between **full-siblings** in a diploid outbreeding species (female XX, male XY)

| Location of Gene | M → M | M → F | F → F | F → M |
|---|---|---|---|---|
| Autosome | ½ | ½ | ½ | ½ |
| X chromosome | ½ | ½ | ¾ | ¼ |
| Y chromosome | 1 | 0 | — | — |
| Extranuclear | 1 | 1 | 1 | 1 |

M = male; F = female. (from Trivers 1985)

- Note that the X-chromosome has 8% of all genes, but they are inherited in a sex-biased fashion.
- The Y-chromosome has very few genes (humans: 89 of 22,250); these are inherited asexually, father to son.
- What are the implications and possibilities?



An example from the **sex** chromosomes

- A mutant allele appears on the Y-chromosome that favors altruistic interactions between brothers whenever B > C (since $r$ = 1 between brothers for the Y-chromosome).
- This will spread at first, largely *because* $r$ = 1; i.e., higher than between males and any other category of relatives.
- But genes at most other loci – the autosomal ones and those on the X-chromosome – will be harmed by its spread. It's an ***outlaw gene***.
  - Selection will favor the evolution of alleles on the other chromosomes that shut down the selfish mutant, such as a protein that binds to the Y-mutation and prevents its expression.
- Hurst & Hamilton (1992) argued that the ***Y-chromosome is small because of conflict with other genes in the past***, *so most of the Y is shut down*.

But there's an alternate explanation…

**Orr & Kim's (1998) alternative explanation**

- On a non-recombining "proto-Y" chromosome, the overwhelming majority of ***favorable mutations*** suffer **zero probability of fixation**.
- Therefore the fitness of the Y-chromosome lags way behind that of the recombining X-chromosome.
- Eventually the disparity will become so large that selection will favor an *increase* in the expression of X-linked alleles (which are fit), and a *decrease* in the expression of Y-linked alleles (which are unfit).
- So selection reduces the importance – and size – of the Y-chromosome.

**In sum:** ***The Y is small because of its inability to evolve adaptively.***

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**Maybe both reasons are correct.**