

Sample statements in exams and term papers...

- "territoriality evolved for the good of the species."
- "warning coloration helps to perpetuate the species."
- "without echolocation, the bat species would die out."



Tiger scent-marking territory



Echolocating bat



Spotted skunk handstand

Point #1

Natural selection is purposeless and not acting for the good of anything.

We might instead ask at what level selection is operating...

Sample statements in exams and term papers...

- "territoriality evolved for the good of **the species.**"
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Point #2. But why selection at the level of species? Why not the level of:

- ... the individual
- ... the group
- ... the population
- ... the subspecies
- ... **the species**
- ... the species community
- ... the ecosystem

Or, going in the other direction in terms of organization, why not selection at the level of:

- ...individual
- ...organ
- ...tissue
- ...cell
- ...chromosome
- ...gene

Today, we will discuss selection at the level of the:

- ...individual
- ...group
- ...gene

Where does selection on animal behavior actually operate?

Darwin's theory of natural selection focused mainly on which of these levels?



Example -- nectar foraging in bees



Darwin: "Suppose a new flower appears in the environment, which has a **corolla** that is longer than the average tongue length of the local bees."

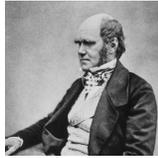


The bee's proboscis increases in length under natural selection:



1. **Individual** bees in a population vary in proboscis length.
2. New flower type with long corollas appears in the habitat.
3. **Individuals** with long probosces reproduce more successfully than **individuals** with short ones.
4. If variation in proboscis length is partly genetically-based, then **individuals** with long probosces will increase in frequency in next generation.

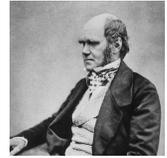
Darwin's theory of natural selection focused mainly on the level of the Individual.



"... individual differences in the curvature or length of the proboscis... might profit a bee or other insect, so that certain individuals would be able to obtain their food more quickly [from flowers] than others..."

-- C. Darwin, 1859 "The Origin of Species"

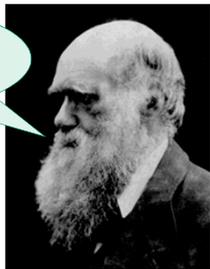
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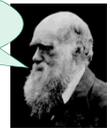
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For the love of Pete, it's the individual!



BUT...

For the love of Pete, it's the group!



Darwin & Group-Level Selection

Darwin invoked group selection to explain evolution of moral virtue in primitive human societies.

He argued that bravery was selected against within a group, but selected for between groups.

For next 100 years, biologists appealed freely to group selection, especially for traits like altruism.

"... the greatest benefits of sociality arise from its capacity to override the advantage of the individual members in the interests of survival of the group as a whole."

-- Wynne-Edwards, 1962

Wynne-Edwards believed that individual traits reflected group-selected adaptations for **population regulation**.



Lemming Suicide as Population Regulation?

"lemming suicide evolves at the level of the population, functioning to keep populations from going extinct."

White Wilderness video:

<http://www.youtube.com/watch?v=xMZlr5Gf9yY>



Lemming suicide is a **MYTH**. Lemmings do **NOT** periodically hurl themselves into the sea.

Cyclical explosions in population cause lemmings to migrate to areas of lesser density.

When migration occurs, some mortality occurs.

Disney's *White Wilderness* filmed in Alberta, Canada, not native habitat of lemming.

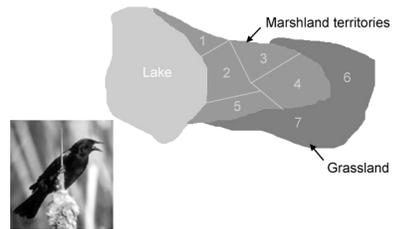
Lemmings purchased from Inuit children for 25 cents each.

Lemmings placed on a rotating platform and **forced off the cliff into the river.**

Let's think about selection operating on territorial behavior:

Territory
an area defended against intruders, generally in protection of a resource

Territoriality in the Red-winged Blackbird



Evolution of Territoriality

Group-Selection Mechanism

Groups with territorial individuals are less likely to deplete resources.

Such groups thus go extinct less often than groups without territorial individuals.

Territoriality increases in frequency in next generation.

Also called demic selection

Evolution of Territoriality

Individual-Selection Mechanism

Individuals which defend territories reproduce more than individuals do not.

Territoriality increases in frequency in the next generation.

Simpler argument... requires fewer assumptions and conditions.

Constraints on Group Selection

1. Group selection weaker due to:
 - a) **low extinction rates** of groups
 - b) **high levels of migration** between groups.
2. Traits favored under group-level selection may be exploited by **cheaters** favored under individual-level selection.

Humorous cartoons suggestive of cheater lemmings

cheater lemmings?

Current Consensus (?)

Individual-level selection thought to be more important than group-level selection.

Group selection may play a role in the evolution of certain group-level traits:

- cooperation
- altruism
- sex ratio

Selection can act at levels below the individual:

...individual
 ...organ
 ...tissue
 ...cell
 ...chromosome
 ...gene complex
 ...gene

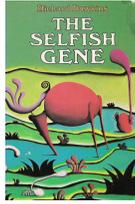
Example: selfish genetic elements may spread despite being costly to individuals bearing them.

Richard Dawkins' latest books: "The God Delusion" and "The Greatest Show on Earth: The Evidence for Evolution"

Also author of:

"The Selfish Gene"

"The Blind Watchmaker"



"The Selfish Gene" addresses **selection at the level of the gene.**

Selection at the Level of the Gene

Example. The **t** haplotype in house mice is a selfish genetic element.

+/+ mice produce normal sperm.

+/t mice produce normal sperm but meiosis is distorted and 95% of the sperm have the **t** haplotype.

t/t mice mainly die as embryos.

Meiotic drive: The **t** haplotype is harmful to individuals, yet persists because it biases its representation in the heterozygote's sperm.



Some **t/+** individuals have no tails. Such mice should have poorer balance and thermoregulation.

Selfish genes generate **intragenomic conflict.**

Example. Mating in *Drosophila* flies

Males transfer substances in seminal fluid that make sperm more competitive (= **spermicides**),

But that harm females, reducing their longevity.

Genes for male function are in conflict with genes for female function.

Lead to '**antagonistic coevolution**' of the genome.



Finally, There's... Kin Selection

Kin selection has elements of selection at levels of gene and individuals.



Concept of Inclusive Fitness

W.D. Hamilton (1964)

an individual increases its fitness either through own personal reproduction or reproduction of genetic relatives

inclusive fitness is fitness due to both forms of reproduction

Concept of Inclusive Fitness *cont'd*

inclusive fitness = direct fitness + indirect fitness

direct fitness component of fitness due to personal reproduction

indirect fitness component of fitness due to reproduction by genetic relatives

Inclusive fitness is critical to understanding the evolution of altruism, cooperation and ... cannibalism (!).

Example A: Belding's ground squirrels

Example B: chimpanzees

Example C: spadefoot toad tadpoles

Altruism
Any behavior that benefits a recipient while incurring a cost to its donor

Examples

- **alarm calls** in ground squirrels
- **helping behavior** in birds & mammals
- **sterile castes** in honey bees, ants and naked mole rats

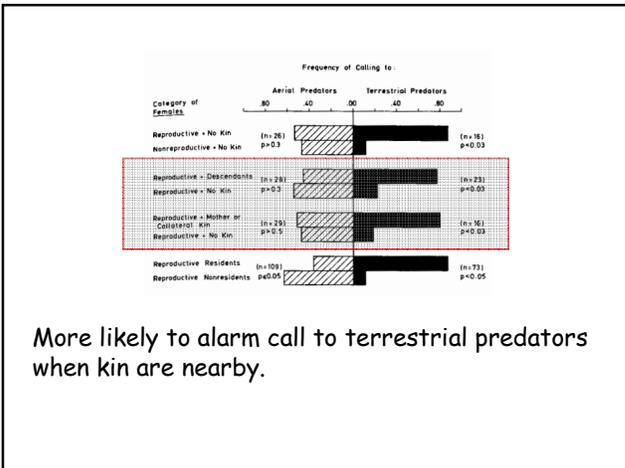
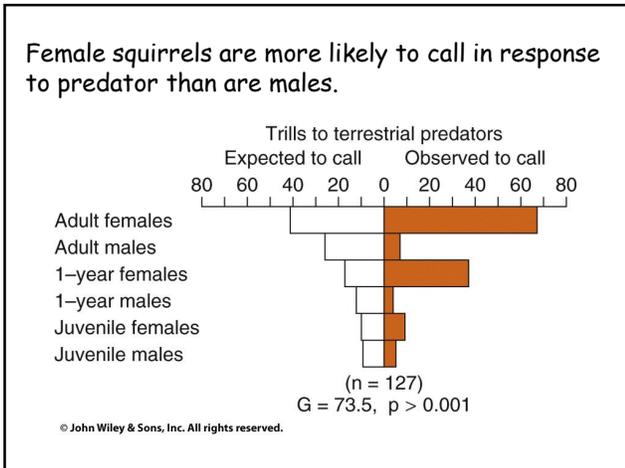


A. Alarm Calls in Belding's Ground Squirrels

Belding ground squirrels

Live in groups. **Females stay in natal group**, males leave. Females are thus genetic relatives.

Squirrels utter alarm calls to alert conspecifics to presence of predator such as hawks or coyotes.



What looks like kissing, involves smelling of glandular odors that signal relatedness.

Females show greater propensity to call when genetic relatives are nearby.

Conditions for altruism towards genetic relatives (kin) are set by **Hamilton's rule**:

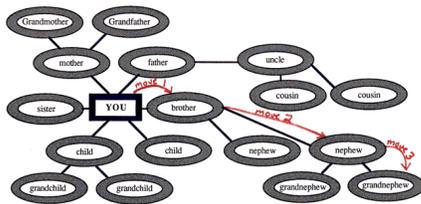
$$b/c > 1/r$$

b = benefits to recipient
c = cost to donor
r = coefficient of relatedness

Relationship	r
mother-offspring	1/2
sister-brother	1/2
uncle-nephew	1/4
cousin-cousin	1/8

This explanation 'takes the altruism out of altruism.'

How to calculate coefficient of relatedness, **r**



Fraction of your genes in relative = $(1/2)^n$
where n = # of "moves" away from yourself

In red you can see that your grandnephew has 1/8 of your genes (as much as a cousin). You can expand this tree as far as you want.

MAY BE ON EXAM!!



Males playing



Females fighting

B. Cooperation between male chimpanzees is greater than cooperation between female chimpanzees.

In chimps, females disperse from the natal troop, whereas males often stay.

Hence, males tend to be more genetically-related to each other, relative to females.

C. Restraint from Cannibalism in Spadefoot Toad Tadpoles

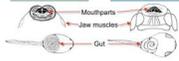


Spadefoot toads common in Southwest; adults underground most of year.

Alternative tadpole phenotypes



Tadpoles can be omnivores or carnivores.



Shrimp ingestion triggers development of carnivore morph.

Carnivores will cannibalize smaller tadpoles;
But are less likely to cannibalize kin!
AND... less likely to become carnivores if surrounded by kin!

Summarizing, we have discussed natural selection at the levels of:

- ...individual
- ...group
- ...gene
- (...kin)

In most cases, we will assume individual-level selection is acting on behavior.