

9.20 M.I.T. 2013

Lecture #20

**Sociobiology subject matter**

John Alcock, *The Triumph of Sociobiology*, ch 2:

## **Fitness**

1. Define “fitness” as the term is used by sociobiologists. What are fitness costs and fitness benefits? Give examples.

p 24

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## Fitness

1. Define “fitness” as the term is used by sociobiologists. What are fitness costs and fitness benefits? Give examples. p 24

**Fitness** is defined as the number of surviving offspring, **or**, more precisely, as the number of an individual’s own genes passed to surviving offspring.

**Fitness costs** reduce probability of gene survival.

**Fitness benefits** increase probability of gene survival.

**Example:** Think of possible fitness benefits & costs to a female bird when she engages in extra-pair copulations (EPCs). Are these the same for a male bird? Then think about how you could gather information to test these possibilities. (This is what sociobiologists do.)

John Alcock, *The Triumph of Sociobiology*, ch 2:  
**Misconceptions**

2. What are the misunderstandings of sociobiological thinking we can see in the statements of Derek Bickerton, Michael Rose and William Kimler, quoted by Alcock? (pp 25-27)

# Misconceptions, in brief

Derek Bickerton

“When a bird practices what zoologists call ‘extra-pair copulation,’ can we really call this adultery?...The intent of the two activities is completely different...”

Michael Rose

“...there is the fundamental problem that, if most people calculate Darwinian plans of action, they certainly aren’t aware of it introspectively. Net Darwinian fitness doesn’t figure in the great lyric poems...”

William Kimler

“...criticizes the sociobiological claim that adulterous women have sometimes raised their genetic fitness by cuckolding a social partner, on the grounds that [she might] be seeking more emotional satisfaction ... rather than a simple genetic benefit.”

# Remember:

- *The mistakes of Bickerton and Rose*: Fitness is not about conscious intent.
- *Kimler's mistake*: He failed to recognize that proximate motivational states are distinct from ultimate results.
- In the words of John Alcock: “Understanding the difference between proximate and ultimate hypotheses, which are different but complementary to one another, can help us avoid the kind of confusion evident in Kimler’s complaint about sociobiology.” (p 28)

John Alcock, *The Triumph of Sociobiology*, ch 2:  
Proximate vs ultimate

3. Contrast proximate mechanisms/causes and ultimate outcomes for a specific behavior.

Example: the human tendency to eat high-fat, sweet foods.

Consider psychological and physiological / anatomical mechanisms (proximate causes) and, separately, the reasons for their evolution.

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## Proximate vs ultimate

3. Contrast proximate mechanisms/causes and ultimate outcomes for a specific behavior.

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Example: Human desire to eat high fat, sweet foods:

Ultimate causes: This evolved to increase genetic fitness, and genetic fitness does not involve long-term survival, at least, not very much. (Just how much is a subject of debate.)

What are advantages of fat and sweet foods?

Such advantages are what caused us to evolve innate preferences for them.

Proximate causes: Taste effects on hunger & eating (IRMs); brain mechanisms, hormonal mechanisms, feeding reflexes & FAPs.

John Alcock, *The Triumph of Sociobiology*, ch 2:  
George C. Williams vs Wynne-Edwards

4. What was the thesis of Wynne-Edwards in his 1962 book, that was forcefully countered in 1966 by George C. Williams?

Describe Williams' counter thesis, which is a key for understanding modern sociobiology (since 1975).

Wynne-Edwards' book was very popular, and the views expressed there persisted in public perceptions. They persist even today.

Wynne-Edwards VC (1962) *Animal Dispersion in Relation to Social Behaviour*.  
Williams GC (1966) *Adaptation and Natural Selection*.

# George C. Williams vs Wynne-Edwards on how evolution works:

Wynne-Edwards ('62), *Animal Dispersion in Relation to Social Behavior*. Interpreted almost every aspect of social behavior to be altruistic self-sacrifice that advances the **welfare of the species** (*Alcock, p 29*)

George C. Williams ('66), *Adaptation and Natural Selection*.  
“presented the counter thesis that evolved adaptations, including behavioral ones, were extremely unlikely to promote the long-term survival of entire populations or species *at the expense of individual reproduction.*”

See p. 30: his thought experiment

- But what about the effects of overcrowding that result in population declines?
  - They are caused by physiological and behavioral effects of stress
  - Examples: overactive adrenal gland secretions, decreased immune-system function, increased social conflict
- These effects caused reduced fertility, which makes them constitute a “**Darwinian puzzle**” of interest to sociobiologists.
- NOTE: E.O. Wilson (1975, 1980) discusses the issue of group selection extensively after citing G.C. Williams (1966). He evaluates conditions that favor inter-demic selection for genes promoting altruism. The issue is a complex one.
- Since 1975, most sociobiological studies have not focused on such group selection. This has begun to change in the last few years

John Alcock, *The Triumph of Sociobiology*, ch 2:  
Darwinian puzzles

5. What is a “Darwinian puzzle”? Give an example, and also a solution to the puzzle.

p 32f:

“Anything that appears to reduce an individual’s chances of reproducing successfully, even by a small degree, becomes by definition a Darwinian puzzle.”

## Darwinian puzzles

- Why do whirligig beetles congregate so much when large groups of them are attacked more often than smaller groups?
  - They also pay a price in reduced reproduction: However:
  - Attacks were lower per individual as group size increased. This outweighs the costs.
- Why do humans love pet dogs so much, although dogs can spread disease and cause lethal bites?
  - Is it a maladaptive side effect of proximate mechanisms that evolved for other reasons?
  - e.g., caregiving responses; need for companionship; desire for protection; human responses to loyal friendliness...

Think about what dogs must have contributed to small hunter-gatherer groups.

John Alcock, *The Triumph of Sociobiology*,

**Appendix ch 2, Q2: Challenges for a Darwinian adaptationist**

6. Which behavior of specific animals would challenge a Darwinian adaptationist (a sociobiologist) most? Study the four descriptions. [P 225-226](#)

**Appendix ch 2, Q2: Challenges for a Darwinian adaptationist**

6. Which behavior of specific animals would challenge a Darwinian adaptationist (a sociobiologist) most? Study the four descriptions. (on p 225-226)

**A.** The arduous journey of an ocean-dwelling salmon to locate and swim up a stream in order to breed entails very high costs. What are the fitness benefits?

**C.** Birds accept eggs from non-mates, even from another species, and care for them, feed the hatchlings, etc. There seem to be no fitness benefits, at least not immediate ones. The behavior may be a maladaptive side effect of caregiving FAPs.

But remember the research findings on spotted cuckoos in Spain (discussed in Lecture 9).

The fitness benefits are easier to understand for **B** and **D**.

But easiest for **D**.

John Alcock, *The Triumph of Sociobiology*,

**Appendix ch 2, Q3: Speculation about human warfare**

7. Why would evolutionary biologists (like sociobiologists) object to the speculative argument of Marvin Harris about the origins of human warfare? (p 226)

Harris, a cultural anthropologist, argued that human warfare "stems from the inability of preindustrial peoples to develop a less costly or more benign means of achieving low population densities and low rates of population growth" needed to prevent overexploitation of essential resources.

John Alcock, *The Triumph of Sociobiology*,

**Appendix ch 2, Q3: Speculation about human warfare**

7. Why would evolutionary biologists (like sociobiologists) object to the speculative argument of Marvin Harris about the origins of human warfare?

**Harris makes species benefits more important than benefits to the individual.**

# More from E.O. Wilson's "Sociobiology" (1975, 1980)

Continued from previous class (see the  
last few slides of class 21)

First, review the summaries from the last class.

## Ch 1. THE MORALITY OF THE GENE

Please see pages 3 and 4 in:

Wilson, Edward O. *Sociobiology: The New Synthesis*.  
Harvard University Press (1980).

## Ch. 2. ELEMENTARY CONCEPTS OF SOCIOBIOLOGY

- Definitions

- **Population**

- A set of organisms belonging to the same species and occupying a clearly delimited area at the same time.
    - The population is bounded by a zone of sharply reduced gene flow. (Compare with “society” below.)

- **Deme:** The special population used by model builders, defined as the smallest local set of organisms within which interbreeding occurs freely.

- **Species:** a population or set of populations within which the individuals are capable of freely interbreeding under natural conditions.

- **Society:** The society is bounded by a zone of sharply reduced communication.

## Ch. 2. ELEMENTARY CONCEPTS OF SOCIOBIOLOGY, continued

- "Social homeostasis": regulation of colony populations, caste proportions, *etc.*
- The **multiplier effect**, p.9.
  - Occurs when a small evolutionary change in individual behavior results in major effects on social behavior patterns.
  - Example: baboons, hamadryas vs. olive: Hamadryas males “possess” particular females long-term, whereas Olive males do so only during estrus periods of females. Result: great differences in social structure.
- The “evolutionary pacemaker”: ++
  - Evolutionary changes in **behavior**\* generally occur before changes in body structures involved in the behavior. Wolfgang Wicker has found good evidence of this in fishes & birds (p 10). \* brain
  - Example: the puffer fishes
    - What starts as adaptive anti-predator behavior has evolved into structural properties of some species within the same group of fishes.

++ when both behavior and body structure change in evolution.

## Ch. 2. ELEMENTARY CONCEPTS OF SOCIOBIOLOGY, continued

- “Adaptive demography”: relative proportions of individuals of different ages and sizes can be influenced by selection in favor of groups\* vs the individual (p. 11).      \* of certain ages
- **Behavioral scaling** (p. 14): With no difference in genetics, behaviors can change as a function of conditions. *E.g.*, increases in population density can drastically alter aggression and territoriality.
- Evolution leads to compromises in social evolution, as adaptations at one level may not be adaptations at another level (*e.g.*, individual, family, population levels).
- **Ultimate vs. proximate causation.**

Next, additional concepts from E.O. Wilson

## Ch 3: The prime movers of social evolution

- **Phylogenetic inertia:** factors that slow evolutionary changes in social behavior: *e.g.*,
  - Reduced genetic variation (as in periods of very reduced population size)
  - **Genetic swamping:**
    - One subgroup begins to change because of altered environmental conditions, but occasional inter-breeding with another subgroup prevents the less adaptive genes from disappearing.
    - Food type and distribution influences social behavior, *e.g.*, distributed, predictable food sources make territorial behavior more adaptive. However, if food sources change, a group may not change its habits because of genetic swamping.

## Ch 3: The prime movers of social evolution

- **Ecological pressure:** specific ecological conditions result in the evolution of specific patterns of social behavior.

### 1) Examples related to anti-predator behavior

- “When spider webs unite, they can halt a lion” (Ethiopian proverb). Colonies are much harder for predators to approach undetected, and attacks have reduced probability of harming any individual.
  - Organized colonies are most effective but an unorganized herd instinct is also effective: cattle, fish, squid, bird flocks, locust swarms (the “selfish herd”)
  - Synchronized breeding: colonial birds; social ungulates
  - Group defense strategies: owlfly larvae confronted by insect predators; guard bees; [guard meerkats]; musk oxen—perimeter defense against wolves; mobbing by certain birds and primates.

## Ch 3: The prime movers of social evolution

- **Ecological pressure:** specific ecological conditions result in the evolution of specific patterns of social behavior.

### 2) Examples related to foraging:

- Groups/coalitions & cliques can increase competitive ability in feeding
- Increased feeding efficiency by social behavior:
  - *Imitative foraging:* (birds) territories form when food is evenly distributed
  - *Cooperative foraging:*
    - Feeding flocks form when food is in unpredictable patches.
    - *Cf* pack-hunting mammals, ant cooperation, honeybee communication.
    - Large prey makes cooperative hunting more adaptive for carnivores.
- Chronic food shortages make solitary, anti-social behavior more likely (e.g., the moose)

## E.O. Wilson's "Sociobiology" (1975, 1980)

### Ch 4: The relevant principles of population biology (selected)

- Calculation of the inbreeding coefficient, which is the same as the coefficient of kinship: use of **“path analysis”**
  - Represents the probability that both alleles at one locus are identical because of common descent.

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