

9.20 M.I.T. 2013

Lecture #24

Discoveries of sociobiology

Alcock ch 6:

What have sociobiologists discovered?

Two major topics:

- Changes in the field of animal behavior because of the influence of the sociobiological approach
- Examples of Darwinian puzzles solved

John Alcock, *The Triumph of Sociobiology*, ch 6:

A change in focus within behavioral science

1. What big change in animal behavior research occurred after about 1970?

pp 94-95

This was after the publication of *Adaptation and Natural Selection* by George C. Williams in 1966.

John Alcock, *The Triumph of Sociobiology*, ch 6:

A change in focus within behavioral science

1. What big change in animal behavior research occurred after about 1970? pp 94-95

See Table 6.1, p 95.

Shift in emphasis from proximate causation to ultimate causation, i.e., adaptive significance.

An exception was in the behavioral studies by scientists focused on brain mechanisms. Some of them work in the area of “neuroethology.” Others use animals as models for the study of specific brain structures or specific types of learning.

John Alcock, *The Triumph of Sociobiology*, ch 6:

Lorenz' writings about evolution

2. What view of evolution was presented by the famous ethologist Konrad Lorenz in his 1966 book, *On Aggression*, a view of Darwinian theory that has been rejected by sociobiologists?

Why did this mistake not impede K.L. in his major studies?

John Alcock, *The Triumph of Sociobiology*, ch 6:

Lorenz' writings about evolution

2. What view of evolution was presented by the famous ethologist Konrad Lorenz in his 1966 book, *On Aggression*, a view of Darwinian theory that has been rejected by sociobiologists?

Lorenz wrote about species benefits, vs G.C. Williams* (1966) who argued for the dominance in evolution of individual benefits, meaning the survival and propagation of specific genes carried by the individual.

Why did this mistake not impede K.L. in his major studies?

Lorenz focused on proximate questions.

**Adaptation and Natural Selection (1966)*

Lorenz' writings about evolution:

- In his book *On Aggression* (1966), his theoretical orientation is “group selectionist”. When he discusses purpose in evolution, he writes, e.g., “...its explicit function was selected ... because of its species-preserving value” (p 29 in *The Foundations of Ethology*, 1981).
- However, when he writes about genetic variation, he discusses the survival of individuals (p 26), and quotes Eigen (1975), “Life is a game in which nothing is stipulated but the rules.”

This was fairly similar to E.O. Wilson (1975, 1980), on “the morality of the gene”:

- See page 3.
 - At first this seems ridiculous—until you realize that “purpose” from the standpoint of biological evolution is very restricted. Evolution follows a blind and simple rule. When we think about consciousness and the great ontological questions, we place ourselves outside the realm of that rule.
- The brain centers that are responsible for emotions have evolved by natural selection. ***The hypothalamus and limbic system are engineered to perpetuate DNA.***
- But Wilson is also “group selectionist,” albeit in a way that comprehends molecular genetics:

See quotation on next slide.

From E.O. Wilson, *Sociobiology, the abridged edition* (1980)

- See p 3-4
- Group selection

John Alcock, *The Triumph of Sociobiology*, ch 6:

Wm D. Hamilton's analysis of altruism in 1964 (before Wilson's book)

3. In 1964, William D. Hamilton published a very influential paper* that included an analysis of the altruistic behavior of sterile workers in colonies of social insects. What knowledge that had been unavailable to Charles Darwin did Hamilton apply to this problem? (p 96)

* The genetical evolution of social behavior, I, II. *Journal of Theoretical Biology*, 7: 1-52.

Wm D. Hamilton's analysis of altruism in 1964 (before Wilson's book)

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Unlike Darwin, Hamilton had knowledge of genes: He focused on the genetic consequences of extreme altruism.

He pointed out that, in a colony of social insects, males are haploid, but females are diploid. If a queen's eggs are all fertilized by one male, then sister offspring share 50% of the mother's genes, 100% of the father's, hence 75% with each other.

This should promote altruistic behavior of female workers toward sisters who are future queens. It increases chances of reproduction of their own genes. **Examples in following slides.**

There are alternatives to theory of inclusive fitness, but they have not

- What are the alternatives to Hamilton's theoretical analysis in explaining the evolution of a sterile worker class in social insects?

See the article posted online:

“The evolution of eusociality” by Nowak MA, Tarnita CE & Wilson EO (2010), *Nature* 466: 1057-1062.

The authors present an alternative to the "inclusive fitness" theory, but not to natural selection.

See also: Wilson DS and Wilson EO (2007) Rethinking the theoretical foundation of sociobiology. *Quarterly Review of Biology*, 82: 327-348.

[These authors (not related) discuss the rejection of group selection, and argue for a return to it.]

Altruism in naked mole rats

4. How are naked mole rats similar to the Hymenoptera (social insects) in a way that leads sociobiologists to predict extreme altruistic behavior in these mammals? p 97-98

One queen, several male consorts.

Groups with strong genetic relatedness

Workers are siblings or half siblings, but inbreeding increases genetic relatedness.

-- The predictions of extreme altruistic behavior have been verified.

Naked mole rat



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Social insect worker preference

5. Why did Robert Trivers and Hope Hare (1976) predict that in colonies of social insects, workers would care more for future queens than for future drones (males)? [See p 101](#) [Back to the genetics](#)

Social insect worker preferences

- Genetics of the social Hymenoptera

(See p 96-97 on Hamilton; also fig 6.1, and p 101 top):

- Fertilized eggs produce females;
- Unfertilized eggs produce males.
- One result: A female is more closely related to her sisters than she is to her daughters as well as to her brothers.

✿ Thus, a female worker's genetic fitness benefits more if she raises sisters than if she raises brothers or daughters.

(This reveals a reason why a sterile worker caste could evolve.)

Ant workers care about mother's mating

6. Why should it matter to European wood ant workers whether their mother mates with one male or with several?

p 102

The ant workers behave very differently. This presents us with a puzzle. How can the puzzle be solved?

Why should it matter to European wood ant workers whether their mother mates with one male or with several? *p 102*

- Because the gene calculations are very different if she mates with one male or more than one.
 - One male: The female workers share up to 75 % of genes with sisters, and only 25% with brothers.
 - Two males: Workers who are half-sisters share only 25% of genes, the same as with brothers.
 - Somehow the workers know, because proportional investment in females by workers does depend on the mother's mating status.
- *Sisters get more care only if mother is monogamous.**
- “No one would ever have looked for such a thing if they had not been educated by Hamilton and Williams.” (Key papers: W.D. Hamilton, 1964; G.C. Williams, 1966.)

* Sundstrom, Chapuisat, & Keller (1996) Conditional manipulation of sex ratios by ant workers: A test of kin selection theory. *Science*, 274: 993-995.

Even more surprising:

Red fire ant colonies with > 1 queen:

- Only queens that are heterozygous for one particular gene are allowed to survive and reproduce. *See p 102-103.*

The gene is Gp-9, with two alleles, B and b:

- Only Bb queens are the ones in the breeding pool.
- Those with bb do not survive to reproductive age.
- Those with BB genotype are attacked and killed by mobs of workers with Bb genotype.
- Workers with BB do not participate.

This behavior could not be explained without the gene-counting of sociobiologists.

Evolution of male behaviors to counter the influence of female choice:

John Alcock, *The Triumph of Sociobiology*, ch 6:

The male's staying near his mate (damselfly)

7. What is the explanation for why a male damselfly stays near a female he has first mated with rather than fly off in search of other females to mate with?

What did G. A. Parker, in 1970, call this type of phenomenon?

Would you expect it to be widespread across various species?

p 104f

John Alcock, *The Triumph of Sociobiology*, ch 6:

The male's staying near his mate (damselfly)

7. What is the explanation for why a male damselfly stays near a female he has first mated with rather than fly off in search of other females to mate with?

What did G. A. Parker, in 1970, call this type of phenomenon? “Mate guarding”*

Would you expect it to be widespread across various species? Yes, **if the females remain receptive after mating and can still be impregnated**

p 104f

* Not to help her but to prevent her from mating with other males.

Blue damselfly



Courtesy of [Inside Lancashire](#) on Flickr. License CC BY-NC-SA.

John Alcock, *The Triumph of Sociobiology*, ch 6:

Toxic inseminations (fruit flies)

8. Why have male fruit flies evolved so they inject chemicals that harm their mate, chemicals injected along with their sperm? Explain in terms of evolutionary “fitness”, following the logic of George C. Williams (1966).

p 109-112

Toxic inseminations (fruit flies)

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p 109-112

From the perspective of the male, what counts is the number of eggs capable of hatching that he inseminates. It is in the interests of **his** genes to destroy sperm from other males, even if this entails reducing the genetic fitness of the female—by shortening her life or by reducing the total number of her eggs (as long as this reduction is not extreme).

REVIEW of a phenomenon we met previously:

John Alcock, *The Triumph of Sociobiology*, ch 6:

Making sense of peculiarities of mating behavior

9. Explain the evolutionary logic of the mating behavior of hanging flies studied by Randy Thornhill (1976).

Why does the male present the receptive female with a gift of food, like a dead moth, and why does the gift have to be above a certain size to be most effective?

See p 113-115; figure 6.10

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John Alcock, The Triumph of Sociobiology, ch 6:

Making sense of peculiarities of mating behavior

Hanging flies, findings of Thornhill (1976):

- If the food is all eaten before the male has finished, or even begun, transferring sperm, the female uncouples and flies off to find a male with a larger food offering.
- After the sperm transfer is complete (in 20-25 min), the male and female often fight for what remains of the food.
- **CONCLUSION**: The interaction between male and female hanging flies is “marked with genetic conflict, as each individual jockey for maximum personal reproductive gain and thus maximum genetic success.”

Mate choice by females, after Thornhill (and Williams):

“Thornhill’s papers on the topic of female choice and conflict between the sexes marked the start of an era, still continuing, in which these issues have been actively explored. A battalion of adaptationists who have adapted the gene-counting view of evolution are asking questions such as the following:

“How do female mating decisions promote the propagation of their genes?”

“What exactly do females (and their genes) gain when females reject some males in favor of others?”

“How do males manage to compete with rival males in a game whose rules were established by females?” (Alcock, p 115)

John Alcock, The Triumph of Sociobiology, ch 6:
Phenomena of cryptic female choice

10. What is meant by “cryptic female choice” in sociobiology?

Would you expect such phenomena to be found in mammals? In humans?

p 116

John Alcock, The Triumph of Sociobiology, ch 6: Phenomena of cryptic female choice

10. What is meant by “cryptic female choice” in sociobiology?
Would you expect such phenomena to be found in mammals? Humans? p 116

Alcock introduces this with an example from botany (p. 116-118), describing a female flower's response to pollen of various origins. “...as soon as researchers began to employ gene thinking, they started finding fascinating things about plant reproduction that previous workers had overlooked.”

Also discovered: the equivalent of sperm competition by chemicals released from pollen that landed on nearby parts of the style surface.

Cryptic female choice:

Scott (2005) chapter 8)

- Remember the female spotted sandpiper: She leaves her first mate with her first clutch of eggs, and flies off to establish a nest and 2nd clutch with another male.
- However, she may inseminate the second clutch of eggs with stored sperm from the first male!

Related to cryptic female choice:

Scott (2005) chapter 8

- **“Last sperm precedence”**: a strategy that has evolved in females of many species
 - >The ability of female birds to store sperm in tubules near the junction of vagina and uterus: they fill up from the back, so the last sperm in are the first to be released at the time of fertilization.
- **How have males evolved to counter** these cryptic abilities of females?
 - The male dunnock can increase the chances of successful fertilization by his sperm by two behaviors:
 1. Frequent copulation, enhanced when he notices his mate in the vicinity of another male
 2. Pecking of the female’s cloaca prior to copulation → contractions that cause sperm excretion
 - The female can choose whether to allow this behavior, normally conducted as a ritual.

Male countering of female choice:

Other male strategies?

- Sperm removal is common among male invertebrates:
 - Dragonflies and damselflies have penises covered with bristles and horns that the males use to scrub out the female before copulation
- The male bean weevil has a similar penis, but he uses it to lacerate the reproductive tract of the female during copulation. (Think of this as a different type of “toxic insemination.”)
 - This makes it much less likely that she will copulate with another male.
 - It shortens the life of a female from 1 mo to ~10 days
 - Females fight off unwanted male suitors to reduce injuries.

Bean weevil



Courtesy of [Charles Fox](#) on Flickr. License CC BY.



Courtesy of Simon Hinkley and Ken Walker of [Museum Victoria](#). License CC BY.

Female on bean

Other examples of traumatic insemination have been found in:

- Fruit flies (as mentioned previously)
- Bed bugs* →
- Plant bugs
- Spiders

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*See Wolfgang Wickler (1973) *The Sexual Code: The Social Behavior of Animals and Men*, trans. F. Garvie. Garden City: Doubleday; Anchor Press. P 37

Bed bugs are an example of insects, particularly beetles, that practice a violent insertion of sperm into the body cavity of females without using the genital tract. Some females have evolved specialized body parts (thicker outer coverings) to deal with this so there is less trauma to them.

John Alcock, The Triumph of Sociobiology, ch 6:

Phenomena of cryptic female choice

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Next: examples of recent research with primates

Manfred Eberle and Peter M. Kappeler (2004)

Selected polyandry: female choice and inter-sexual conflict in a small nocturnal solitary primate (*Microcebus murinus*)

Behavioral Ecology and Sociobiology, 57(1)

Abstract of report

Sex-specific interests over the maximization of reproductive success lead to an inter-sexual conflict over the optimal mating system in a species. ... We used a small nocturnal primate, the gray mouse lemur (*Microcebus murinus*) to determine the relative importance of female mating strategies on the outcome of this conflict in a species where females are solitary during their activity period. We studied their mating behavior over three consecutive annual mating seasons and determined the genetic relationships among more than 300 study animals to quantify individual reproductive success. ... **females exercised indirect choice for multiple matings. They mated with 1–7 males up to 11 times during their single night of receptivity. As a result, mixed paternity was common but heavier males sired more offspring,...** ...females had a major influence on the outcome of the inter-sexual conflict despite male monopolization attempts.

Ideas about the discovery of two kinds of sperm: “eusperm” & “parasperm,” with different functions:

Spermicide, cryptic female choice and the evolution of sperm form and function (Holman L & Snook RR, *J. Evolutionary Biology*, 19: 1660 - 1670 Published Online: 10 Apr 2006)

Summary of theoretical study on next slide

Ideas about the discovery of two kinds of sperm: “eusperm” & “parasperm,” with different functions:

Sperm competition and cryptic female choice profoundly affect sperm morphology, producing diversity within both species and individuals. One type of within-individual sperm variation is **sperm heteromorphism**, in which each male produces two or more distinct types of sperm simultaneously, only one of which is typically fertile (the 'eusperm'). The adaptive significance of nonfertile 'parasperm' types is poorly understood, although numerous sperm-heteromorphic species are known from many disparate taxa. This paper examines in detail **two female-centered hypotheses for the evolution and maintenance of this unconventional sperm production strategy**. First, we use game theoretical models to establish that parasperm may function to protect eusperm from female-generated spermicide, and to elucidate the predictions of this idea. Second, we expand on the relatively undeveloped idea that parasperm are used by females as a criterion for cryptic female choice, and discuss the predictions generated by this idea compared to other hypotheses proposed to explain sperm heteromorphism. We critically evaluate both hypotheses, suggest ways in which they could be tested, and propose taxa in which they could be important.

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9.20 Animal Behavior
Fall 2013

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