Overview of Lecture: Behavioral Ecology
see the schedule for reading and watching assignments

THE FOLLOWING PREVIEW HAS BEEN APPROVED FOR ALL AUDIENCES

Bullet Points:
• Tinbergen’s 4 whys – bird song
• G & E; nature & nurture
• genotype & social bonding in voles - and in humans
• genotype (XX or XY) and learning in chimps
• gender-typical toys - nature & nurture
• social games – cooperation
• mutualism, reciprocity & harassment
• kin selection
• life is a game – in theory
• prisoners dilemma
• partner choice & punishment

“T’ve tried a lot of life strategies, and being completely self-serving works best for me.”
Learning Goals:

1. Be able to explain “Tinbergen’s four whys” and illustrate with the example of songbird song.

2. Be able to summarize what the study on voles suggests about the role of genetic variants that increase or decrease the abundance of Arginine Vasopressin Receptors in increasing or decreasing levels of social affiliation and bonding.

3. Be able to analyze and explain what the study Sex differences in response to children's toys in nonhuman primates, by Alexander & Hines, suggests about the roles of genotype and environment in the ontogeny/development of toy preferences.

4. Be able to describe four hypothetical explanations for the evolution of altruistic cooperation. Illustrate with the chimp studies by Silk et al. and Engelmann et al. Use the wild turkey study to help explain the kin selection model.

5. Be able to explain the essence of game theory and the essence of the pairwise Prisoner’s Dilemma game and why it creates a social dilemma. How does repeated play with a stable partner encourage cooperation in a pairwise Prisoner’s Dilemma game?

6. Be able to describe the essence of a Public Goods game/problem. Use the study by Gürerk et al. to help explain how institution/partner choice and punishment can encourage cooperation in a public goods game.
Clarifying the meanings of **how** and **why** questions about behavior and other adaptive traits -

“Do you have any why-to books?”
We can think of **behavior** as what an animal does and how it does it, …

including nonmotor (latent) components of behavior

such as learning and memory

*changes of “state” that influence future behavior*

- including hunger, fear, knowledge, skill …

If we consider the development **ontogeny** of any behavioral trait,
we find a series of environmental **“nurture”** and genetic **“nature”** influences
that can ‘interact’ as well as ‘add up’ to influence the phenotype-trait.

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Natural selection favors behavior that enhances survival and reproductive success.

[ but there are many “constraints to perfection,” see: 9/13 Adaptation & Imperfection]

**The debate about biological evolution and human culture remains heated.**

The spectrum of possible human social behaviors

may be constrained by our genetic potential,

but our genetic evolution is also shaped by our cultural environment.  [ex: lactose tolerance]

[see: An introduction to niche construction theory

Tinbergen’s four questions in one system: bird song.

(A) Mechanism \[\text{proximate cause}\]

(B) Current utility \[\text{ultimate function}\]

(C) Development \[\text{ontogeny}\]

(D) Evolution \[\text{phylogeny}\]
All we really know so far is that behavioral genes are not solo players; it takes many to orchestrate each trait. **many genes with small effects**... any single gene may play a role in several seemingly disparate functions. For example, the same gene may influence propensities toward depression, overeating, and impulsive behavior, **[the term for this is pleiotrophy]** making it difficult to tease out underlying mechanisms.
In Voles, a Little Extra DNA Makes for Faithful Mates
Elizabeth Pennisi Science 10 June 2005:Vol. 308. p. 1533

Prairie voles are renowned for being faithful mates ...
On page 1630, E Hammock & L Young report that

- fidelity and other social behaviors in male prairie voles seem to depend on the length of a particular genetic sequence in a stretch of ‘junk’ regulatory DNA between their genes.
- Prairie voles have longer microsatellites near the gene encoding a receptor (V1aR) for the brain chemical vasopressin, and as a result they make more of the receptor than do their more promiscuous cousins - meadow voles. {between species}

Last year, Young's team ...

- caused meadow voles to emulate the faithful ways of prairie voles by adding extra copies of the V1aR gene to a portion of their brains.

Now, Young & Hammock have found that

Oxytocin, Vasopressin, and the Neurogenetics of Sociality [in humans].
Males who are homozygous for [the low output Arginine Vasopressin Receptor 1A...
Wild chimpanzees ... fish for termites with flexible tools they make out of vegetation, ... We find distinct sex-based differences, akin to those found in human children, in the way in which young chimpanzees develop their termite-fishing skills.

It is difficult to tease apart effects of genes & env., esp if genes & env ‘interact.’


Girl chimps learn faster than boys

^ to fish for termites

Daughters pick up their mother’s skills, while sons play rough and tumble.

15 April 2004

MICHAEL HOPKIN

Young female chimpanzees are better students than males, at least when it comes to catching termites, according to a study of wild chimpanzees in Tanzania’s Gombe National Park. While daughters watch their mothers closely, the boys spend more time monkeying around.

**learning skills?**

The discovery mirrors differences in the learning abilities of human children, says the research team behind the study. Girls tend to catch on faster than boys when learning skills such as writing and drawing, they say.

Food for thought: clever chimps get the best snacks. © Alamy.com

These manual tasks are not dissimilar to the chimps’ technique of using a stick to fish for termites, argues Elizabeth Lonsdorf, now at Lincoln Park Zoo in Chicago. Successfully extracting termites from their nest requires a dextrous turn of hand, she says.

Fig 1 Sex differences in wild chimpanzees learning termite-fishing.

**a** % time at the termite mound spent termite-fishing by young chimps.

**b** Daughters' techniques (top) correlate strongly with their mothers'. {lines have + slope ~1}

Females spent more time than males watching their mothers fish for termites

sons' techniques (bottom) do not correlate with their mothers'. {lines have flat slope ~0}

Males spent more time playing at the termite mound

A similar disparity in the ability of young males & females to learn skills has been demonstrated in human children

[ability?? all skills ??]
Sex differences in response to children's toys in nonhuman primates ...


Sex differences in children's toy preferences are thought by many to arise from gender socialization. \{nurture\}

However, evidence from patients with endocrine disorders suggests that biological factors during early development (e.g., levels of androgens) are influential.

In this study, we found that vervet monkeys (Cercopithecus aethiops sabaeus)

For each trial, six toys were placed in the group cage, one at a time, in a random order ... for 5 min.

These toys were categorized as "masculine" toys, "feminine" toys, or "neutral" toys on the basis of evidence that boys are more interested than girls in balls and cars (the "masculine" toy set), girls are more interested than boys in dolls and pots (the "feminine" toy set), and boys and girls are approximately equally interested in books and stuffed animals (the "neutral" toy set).

Videotapes were coded for the duration of contact and approach to each of the toys.

Percent contact scores equaled contact with each individual toy divided by total contact with any of the six toys × 100.
The percent of contact time with toys typically preferred by boys (a car and a ball) was greater in male vervets (n=33) than in female vervets (n=30) (P<.05), the percent of contact time with toys typically preferred by girls (a doll and a pot) was greater in female vervets than in male vervets (P<.01). 

The results suggest that sexually differentiated object preferences arose early in human evolution, prior to the emergence of a distinct hominid lineage.

Sex Differences in Infants’ Visual Interest in Toys.
GM Alexander et al. Arch Sex Behav (2009) 38:427–433 interest in a doll and a toy truck was measured in 30 infants ranging in age from 3 to 8 months using eyetracking …

Exposure to prenatal life events stress is associated with masculinized play behavior in girls.
Barrett et al. 2014. NeuroToxicology 41:20–27. … girls exposed to prenatal life events stress had higher scores on the Preschool Activities Inventory (PSAI), which measures sexually dimorphic [“male”] play behavior.
Because gender differences in toy interests are large and relatively consistent within the United States (Hines and Davis 2018), many parents may seek or suggest simplistic explanations for these differences, such as a genetic basis or identification with a same-gender parent. But when looking at the scientific literature on the topic, the best answer to the question, “Why are there gender differences in children’s toy interests?,” is “It’s complicated.” [recall “Tinbergen’s four why questions”]

Like many areas of individuals’ behavior and preferences, there are biological, cognitive, and social factors to consider. The multitude of factors at play are also not mutually exclusive and interact in ways that are not yet well-understood (Weisgram and Bruun 2018).
London: John Murray. 6th edition;
CHAPTER VI.
DIFFICULTIES OF THE THEORY. pg 162

Natural selection will never produce in a being any structure [or behavior] more injurious than beneficial to that being ... [expected, on average; enlightened self-interest is still self-interest]
Some animals, esp. humans, behave altruistically (unselfishly), in ways that appear to reduce the number of offspring they produce. **How could altruistic behavior have evolved by natural selection?**

**Altruism:** donor pays *cost*, receiver gets *benefit*.

How can altruism be an Evolutionary Stable Strategy & resist cheaters? What ultimate *benefits* compensate for the immediate *costs*?

Four kinds of compensating *benefits* - not mutually exclusive:

1. **Mutualism**: immediately selfish: I'll scratch your back and you scratch mine simultaneously. I'll groom you if you let me eat the tasty tics I find.
   
   Ex: cooperative hunting & defense; market exchanges.

2. **Kin selection**: indirectly selfish: increases copies of genes in future: many more nieces & nephews, if slightly fewer sons & daughters.

   Haldane             - would drown self to save 2 sibs or 8 cousins

   Hamilton's rule: cost to self < benefit to kin · r (coeff of relatedness)

3. **Reciprocity**: ultimately selfish but risky delay between cost and benefit: Direct: If you scratch my back now, I'll scratch yours later. Indirect: via third party observers; reputation, audience effect.

   Note that cash on delivery turns reciprocity into mutualism.

4. **Manipulation**: (a) just plain tricked (nest parasites) (b) offer that can't be refused - harassment & punishment.
Chimpanzees share food for many reasons: the role of kinship, reciprocity, social bonds and harassment …

Joan B. Silk et al. Animal Behaviour 85, May 2013, Pages 941-947

We examined the effects of kinship, relationship quality [reliable friends], reciprocity and the intensity of solicitations [begging/harassment] on the pattern of food transfers in six captive groups of chimpanzees. … after the chimpanzees were provisioned with large frozen juice disks. These disks share some properties with prey carcasses: … they can be monopolized by one individual, but bits can be broken off and transferred to others.

Chimpanzees trust conspecifics to engage in low-cost reciprocity
JM Engelmann et al. 2015 Royal Society B: Biological Sciences 282.
[Given a choice of a little bit of food immediately, or pulling a rope to help a partner get access to a big chunk of food that the partner might then share – or not]
Darwin, C. R. 1872.  
The origin of species by means of natural selection, or the preservation of favoured races in the struggle for life.  
London: John Murray. 6th edition;  
CHAPTER VI. DIFFICULTIES OF THE THEORY. pg 162  
Natural selection will never produce in a being any structure [or behavior] more injurious than beneficial to that being ... [expected, on average; enlightened self-interest is still self-interest]

John Maynard Smith described encountering his mentor J. B. S. Haldane in a pub:  
“J. B. S. Haldane who had been calculating on the back of an envelope for some minutes, announced that he was prepared to lay down his life for eight cousins or two brothers. This remark contained the essence of an idea which W. D. Hamilton, was later to generalise. [as “Hamiltons rule” aka “the altruism equation”]  
What is the logic here? Assumptions?
Assumptions?
In the few species of birds in which males form display partnerships to attract females, one male secures most or all of the copulations. This leads to the question of why subordinate males help ... Hamilton's concept of kin selection, whereby individuals can benefit indirectly by helping a relative, was a crucial breakthrough for understanding apparently altruistic systems. Here I show, using genetic measures of relatedness and reproductive success, that 

\[
\text{[is the increase in kinship-weighted “nieces and nephews” greater than the decrease in kinship-weighted “children” (} rb > c \text{) “Hamilton’s rule”?]}
\]

\[
\begin{align*}
\text{Total offspring} & = 60 \\
\text{Dominant} & \quad \text{Subordinate} \quad \text{Solo} \\
\text{rb} & = ? \\
\text{rb} & = ? \\
\text{c of helping} & = ? \\
\end{align*}
\]

\[
\begin{align*}
c & = 12 \text{ offspring} \\
@ r & = 0.5 \\
= & (12-0) \times 0.5 \\
= & 6
\end{align*}
\]
Game theory is the idealized mathematical study of social interactions.

Most interactions between living, evolving organisms are games, where the payoff to one player depends on the tactics of other players.

Traditional game theory assumes that players are rational actors, always acting in ways that maximize their benefits. Real people are not necessarily like this.

The payoff matrix is the essential way to express a game mathematically.

In zero-sum games, a winner’s gains come at a loser's expense.

Non-zero-sum games can include both win-win and lose-lose situations.

Strategies are the actions [tactics] that players take in a game.

Payoffs are often frequency dependent; that is, they depend on how many people are playing a particular strategy as well as how often a game is played.

Equilibrium is reached when each player has no incentive to play differently.

Game analysis changes when games are played repeatedly. This gives rise to mixed strategies. [including developing trust or retribution]

Game theory can provide insight into many situations, phenomena, and subjects, including biology, sociology, and linguistics.

One of the most interesting conclusions reached in game theory is that rational actions by both players can result in situations in which both players are worse off. The primary example of this is the Prisoner’s Dilemma, …
The essence of cooperation is captured by the **public-goods game.** Each individual can decide whether or not to invest in a common pool. The common pool is increased by some amount and then equally distributed among all group members regardless of whether or not they made a contribution. The optimum outcome for the group occurs if everybody cooperates.

**But the temptation is to 'free ride':** those who don't contribute (defector/cheaters) always get a higher pay-off than cooperators who do contribute. If everyone defect/cheats, however, no one will enjoy the public goods. Self-interest *[myopic selfishness]* is self-defeating! [*The Tragedy of the Commons*]

This social dilemma threatens public enterprises such as social security, conservation of environmental resources or group defence against external threats. *[paying taxes, building roads and bridges, medical research, pollution control … ]*
The well-known "prisoner's dilemma" is a public-goods game for groups of two people.

Two players w/ two tactics: cooperate, defect

\[
\begin{array}{c|c|c}
\text{player 1} & \text{c} & \text{d} \\
\hline
\text{c} & R & S \\
\text{d} & T & P \\
\end{array}
\quad
\begin{array}{c|c|c}
\text{player 2} & \text{c} & \text{d} \\
\hline
\text{c} & R & S \\
\text{d} & T & P \\
\end{array}
\]

\[I've\;translated\;the\;-years\;to\;+payoffs;\;it\;is\;the\;relative\;value\;of\;the\;payoffs\;that\;matters\;here:\;\]
\[
T > R > P > S\quad \text{and}\quad 2xR > T+S
\]

Cooperation is too risky in a single play

... rational actions by both players can result in situations in which both players are worse off.

In repeated play w/ same partner the strategy tit-for-tat (conditional reciprocity) is, on average, a winning strategy because one round of defection is followed by repeated punishment: \([3,1,1,1,1 \ldots] < [2,2,2,2,2 \ldots]\)
Reciprocity is so essential to human sociality that we teach it in fables

The Fox & the Stork

The Fox one day thought of a plan to amuse himself at the expense of the Stork, at whose odd appearance he was always laughing.

"You must come and dine with me today," he said to the Stork, smiling to himself at the trick he was going to play. The Stork gladly accepted the invitation and arrived in good time and with a very good appetite.

For dinner the Fox served soup. But it was set out in a very shallow dish, and all the Stork could do was to wet the very tip of his bill. Not a drop of soup could he get. But the Fox lapped it up easily, and, to increase the disappointment of the Stork, made a great show of enjoyment.

The hungry Stork was much displeased at the trick, but he was a calm, even-tempered fellow and saw no good in flying into a rage. Instead, not long afterward, he invited the Fox to dine with him in turn. The Fox arrived promptly at the time that had been set, and the Stork served a fish dinner that had a very appetizing smell. But it was served in a tall jar with a very narrow neck. The Stork could easily get at the food with his long bill, but all the Fox could do was to lick the outside of the jar, and sniff at the delicious odor. And when the Fox lost his temper, the Stork said calmly:

Do not play tricks on your neighbors unless you can stand the same treatment yourself.
Dear Enemies and the Prisoner's Dilemma: Why Should Territorial Neighbors Form Defensive Coalitions?

THOMAS GETTY

Integrative and Comparative Biology, Volume 27, Issue 2, 1 May 1987, Pages 327–336,
https://doi.org/10.1093/icb/27.2.327
Published: 01 August 2015

Abstract

Game-theoretic arguments are used to derive two new hypotheses to explain why territorial residents so consistently defeat potential usurpers. Both hypotheses are based on help from established, familiar neighbors. The first hypothesis follows simply from Krebs' (1982) assertion that the value of a territory to a usurper must be decremented by the costs of negotiating dear-enemy relationships with the remaining neighbors. An implication is that the remaining neighbors will also have to pay these renegotiation costs if the usurper succeeds. The first hypothesis is that it may benefit a territorial animal to help its established neighbors defend so it can avoid having to renegotiate territorial boundaries with a new, unfamiliar neighbor. This hypothesis assumes net positive benefits to helping without requiring reciprocation.

The second hypothesis requires reciprocation to compensate for immediate net costs of helping. An animal should help its neighbors fight off usurpers only if the neighbors will reciprocate. This hypothesis is based on the prisoner's dilemma game and builds on Axelrod's (1984) work. Cooperative defense (reciprocal help) can be an evolutionarily stable strategy (ESS) if several conditions are met. One critical condition is that the relationship between neighbors is relatively stable. Cooperative defense should help established neighbors retain their territories, and should therefore be a cause, as well as a consequence of stability. It is suggested that the necessary conditions are not very restrictive, that they are often met in nature, and that shared defense is observed but not recognized as such.
Cooperation, Punishment, and the Evolution of Human Institutions

Joseph Henrich

... cooperative dilemmas, or “public goods” problems, involve situations in which individuals incur a cost to create a benefit for the group.

... think of recycling, buying a hybrid car, valor in combat, voting, and donating blood.

The dilemma arises from free-riders who enjoy the group benefits ... without paying the costs.

... free-riders can profit and proliferate, leading to the eventual collapse of cooperation.

On pg 108 of this issue, Gürerk et al. take an important step in understanding how self-sustaining cooperative institutions may have emerged ...

In their experiment, the “players” choose between two different “institutions.” In one, \{ sanction free SFI \} players can contribute money to a group project. The sum of all contributions is augmented by a fixed percentage and then is divided equally among all players, regardless of their contributions.

The other “sanctioning” institution \{ SI \} is very similar, except players can pay to punish (reduce the payoff of) other players. ...

Players could, choose their institution for the next interaction. Initially, most players picked the institution without sanctioning ...

After a few interactions ...
The Competitive Advantage of Sanctioning Institutions

Profound empirical evidence shows that the possibility of sanctioning norm violators stabilizes human cooperation at a high level, whereas cooperation typically collapses in the absence of sanctioning possibilities. Would a sanctioning institution deliberately be adopted when individuals can choose between a sanctioning {SI} & sanction-free {SFI} institution?

We show experimentally that a sanctioning institution is the undisputed winner in a competition with a sanction-free institution.

Despite initial aversion, the entire population migrates to the sanctioning institution and strongly cooperates, whereas the sanction-free society becomes fully depopulated.

The findings demonstrate the competitive advantage of sanctioning institutions and exemplify the emergence of social order driven by institutional [partner] selection.

[people choose to join social groups where cheating can be punished – and cheating is rare because of the disincentive.]
Savage Chickens

by Doug Savage

CITIZENS AGAINST ALTRUISM

NOW ACCEPTING DONATIONS