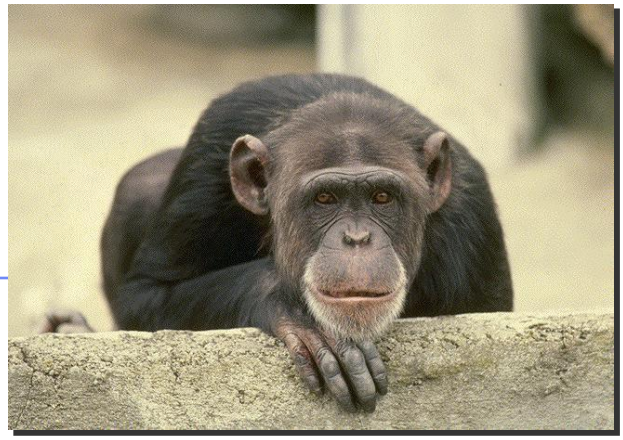
Ch. 51
Animal Behavior



meerkats

What is behavior?

- **Behavior**
  - everything an animal does & how it does it
    - response to stimuli in its environment
  - **innate**
    - inherited, “instinctive”
    - automatic & consistent
  - **learned**
    - ability to learn is inherited, but the behavior develops during animal’s lifetime
    - variable & flexible
      - change with experience & environment

What are some examples?

Why study behavior?

- **Evolutionary perspective…**
  - **part of phenotype**
  - **acted upon by natural selection**
    - **lead to greater fitness?**
    - **lead to greater survival?**
    - **lead to greater reproductive success?**

What questions can we ask?

- **Proximate causes**
  - immediate stimulus & mechanism
  - "how" & "what" questions
- **Ultimate causes**
  - **evolutionary significance**
  - how does behavior contribute to survival & reproduction
    - adaptive value
  - "why" questions

male songbird
→ what triggers singing?
→ how does he sing?
→ why does he sing?

Courtship behavior in cranes
→ what…how… & why questions

→ how does daylength influence breeding?
→ why do cranes breed in spring?

Evolutionary perspective

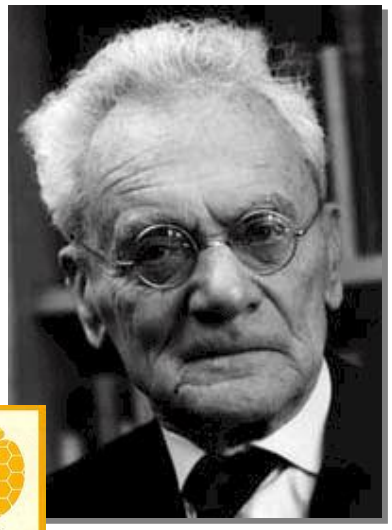
- Adaptive advantage?
  - innate behaviors
    - automatic, fixed, “built-in”, no “learning curve”
    - despite different environments, all individuals exhibit the behavior
    - ex. early survival, reproduction, kinesis, taxis
  - learned behaviors
    - modified by experience
    - variable, changeable
    - flexible with a complex & changing environment

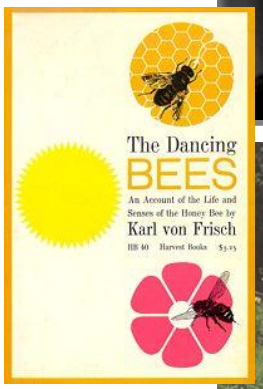
1941 | 1973

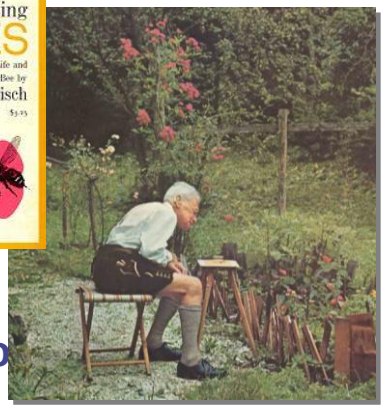
Ethology

pioneers in the study of animal behavior

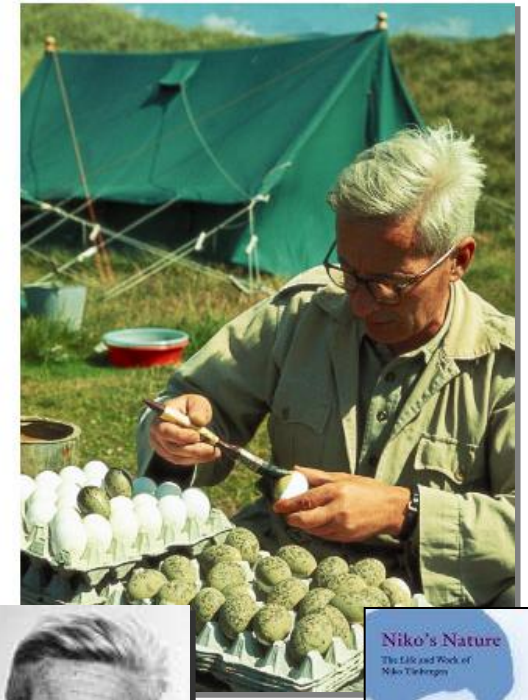
Karl von Frisch

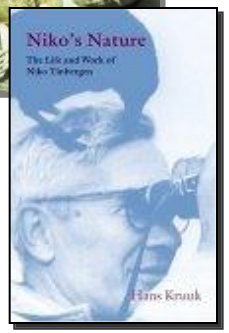




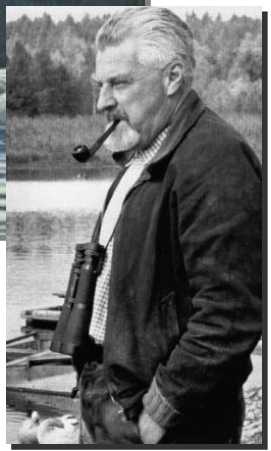


Niko Tinbergen





Konrad Lorenz



Innate behaviors

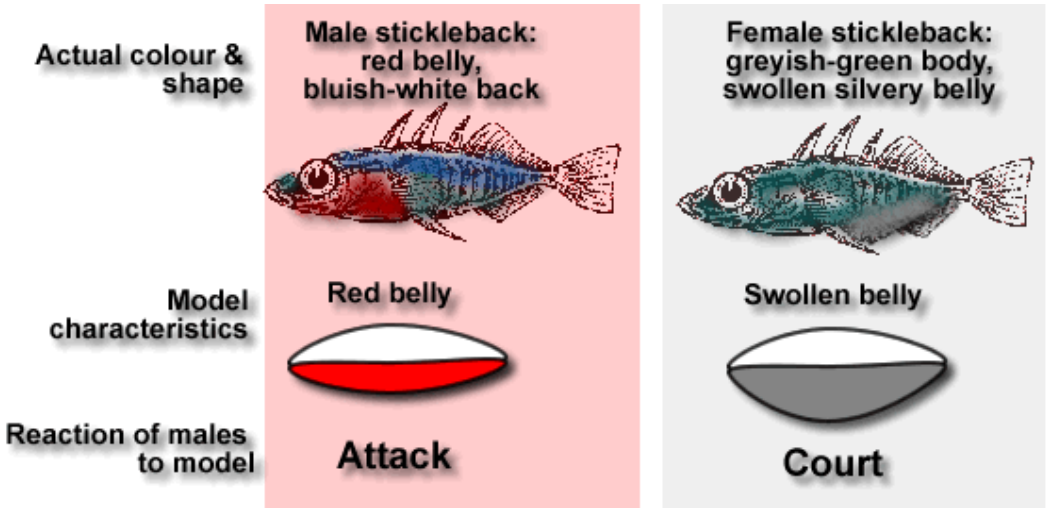
- **Fixed action patterns (FAP)**
  - sequence of behaviors essentially unchangeable & usually conducted to completion once started
  - **sign stimulus**
    - the releaser that triggers a FAP

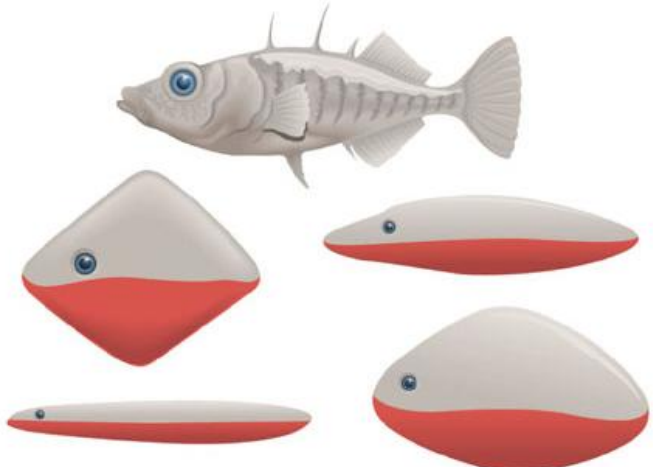
Niko Tinbergen

male sticklebacks exhibit aggressive territoriality

PROXIMATE CAUSE: The red belly of the intruding male acts as a sign stimulus that releases aggression in a male stickleback.

ULTIMATE CAUSE: By chasing away other male sticklebacks, a male decreases the chance that eggs laid in his nesting territory will be fertilized by another male.





attack on red belly stimulus

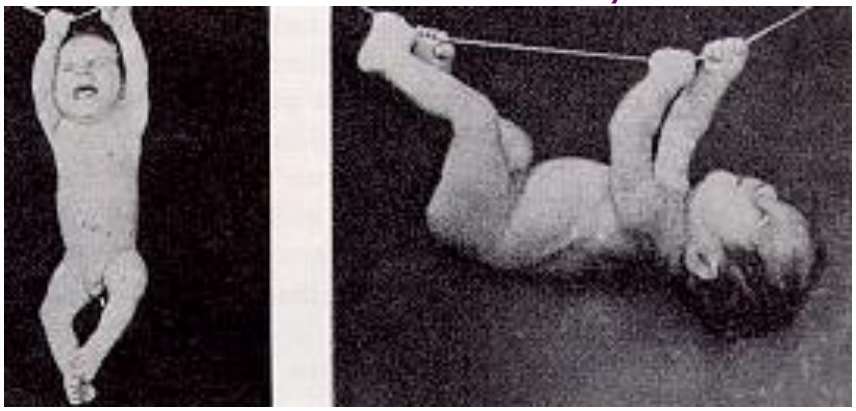
court on swollen belly stimulus

Fixed Action Patterns (FAP)

egg rolling in geese

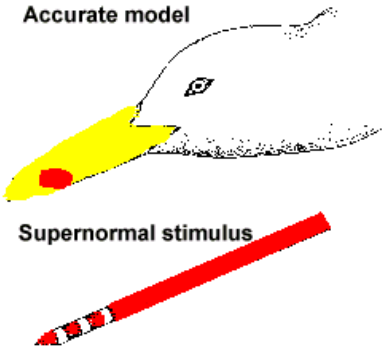
http://www.youtube.com/watch?v=vUNZv-ByPkU

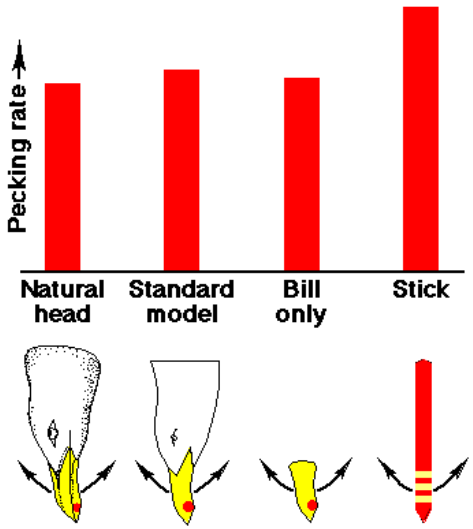
Do humans exhibit Fixed Action Patterns? **Yes, like the new-born behavioral reflex**



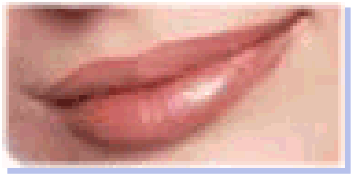
Supernormal Stimulus

- Responding more to a larger sign stimulus
  - adaptation or experimental artifact?



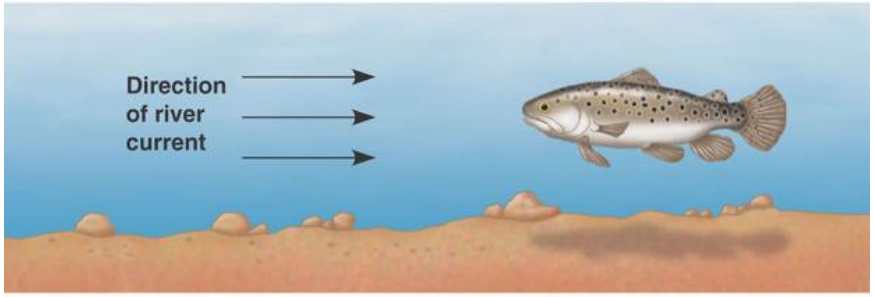


Does lipstick create a supernormal stimulus in humans?

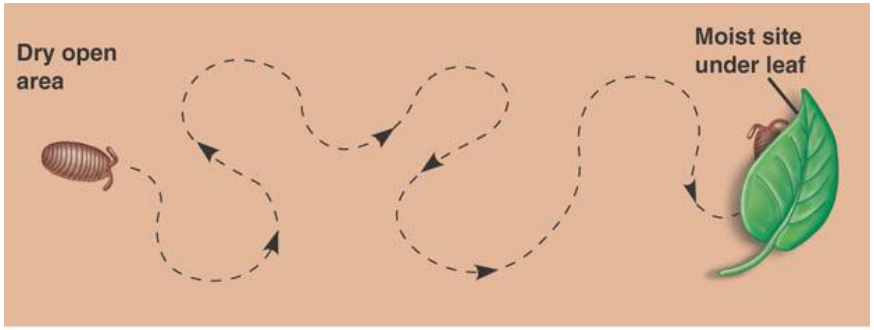


Innate: Directed movements

- **Taxis**
  - change in direction
  - automatic movement toward (positive taxis) or away from (negative taxis) a stimulus
    - phototaxis
    - chemotaxis
- **Kinesis**
  - change in rate of movement in response to a stimulus



(b) Positive rheotaxis keeps trout facing into the current, the direction from which most food comes.

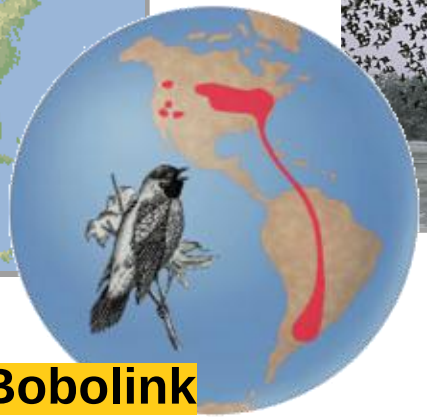


(a) Kinesis increases the chance that a sow bug will encounter and stay in a moist environment.

Complex Innate behaviors-Migration

- Triggered by environmental cues – Δ in sunlight
  - "migratory restlessness" seen in birds bred & raised in captivity
  - navigate by sun, stars, magnetic field, scent, landmarks

Monarch migration



Bobolink

Sandpiper

ancient fly-ways

Golden plover

Behavioral Rhythms

- Behaviors such as migration and reproduction are linked to changing seasons, or a ***circannual rhythm*** – Δ in sunlight, darkness


Swans

- Some behaviors are linked to lunar cycles, which affect tidal movements


Horsehoe crabs

Animal Signals and Communication

- **Communication is the transmission and reception of signals**

Fruit fly courtship follows a three step stimulus-response chain

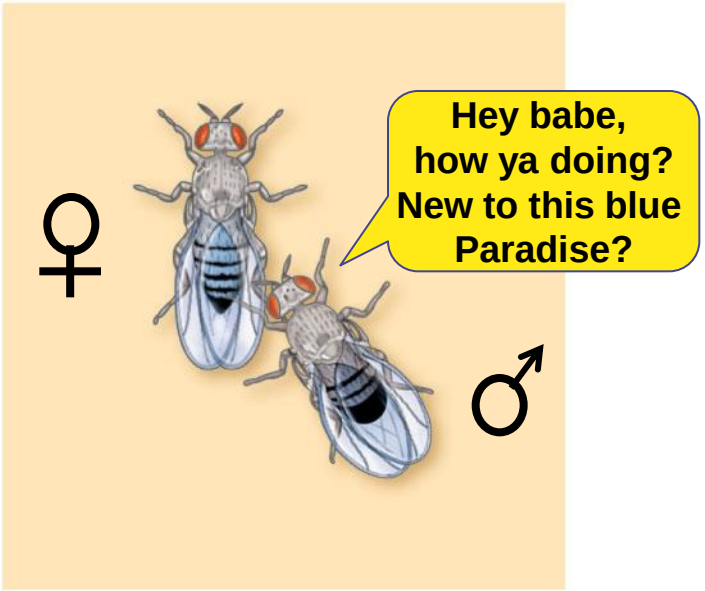
1. Identification! He *smells* the female's chemicals in the air…he *sees* the female and orients his body toward hers

2. The male alerts the female to his presence

- ***Tactile communication***:

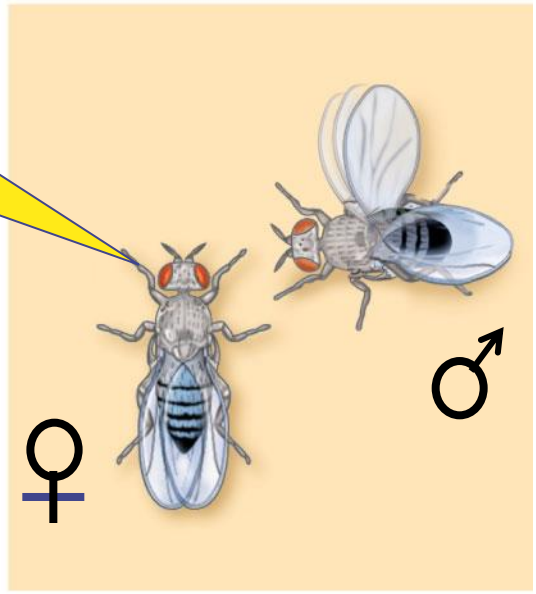
➢ He taps the female with a foreleg

➢ Chemical communication: he chemically confirms the female's identity



3. The male produces a courtship song

- Auditory communication: he extends and vibrates his wing
- If all three steps are successful, the female will allow the male to copulate…if not….



Language

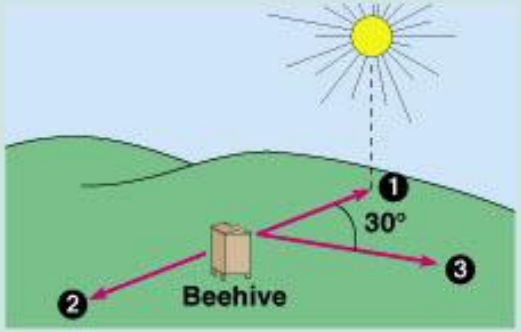
- Honey bee communication
  - dance to communicate location of food source
  - waggle dance

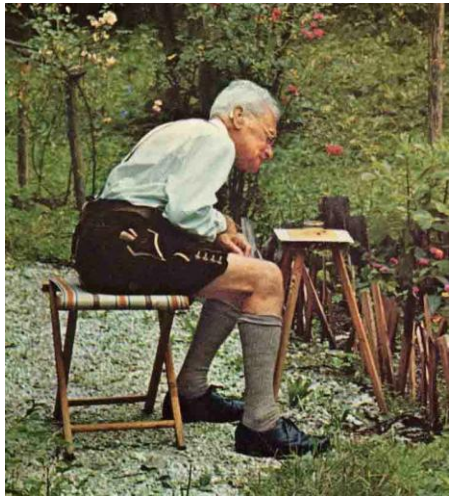
Let's go to the videotape!
http://wildwoodforesthoney.com/VIDEO/video011.htm

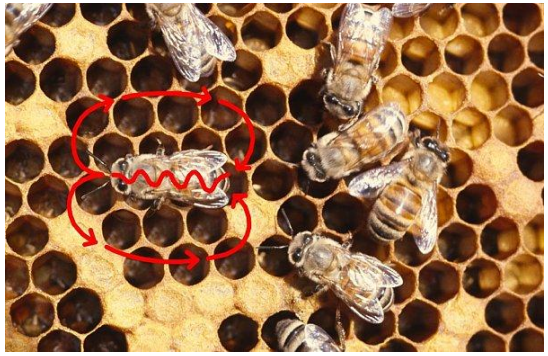
(a) Bees clustering around a recently returned worker

(b) Round dance

(c) Waggle dance

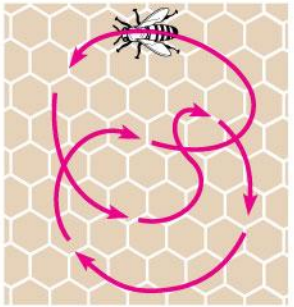




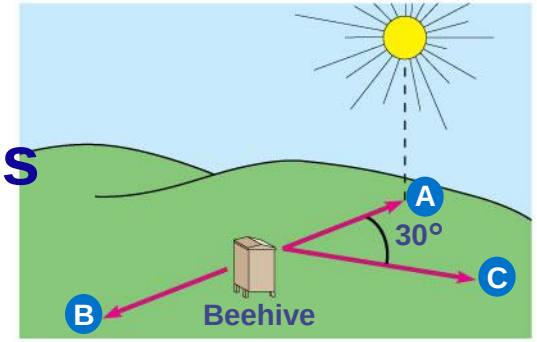


Karl von Frisch

(a) Worker bees



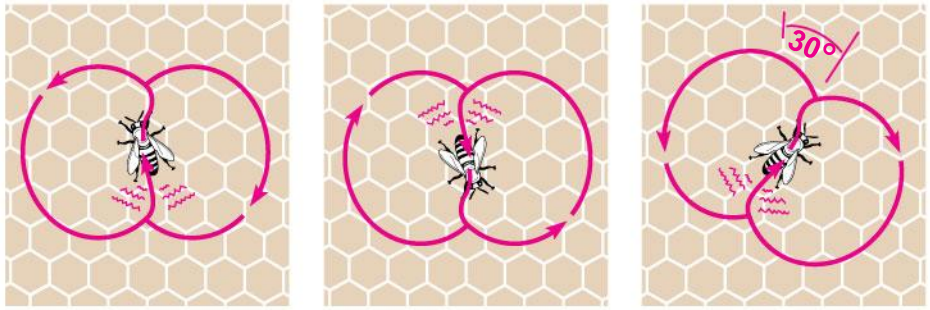
(b) Round dance (food near)



(c) Waggle dance (food distant)

Honeybee Queen

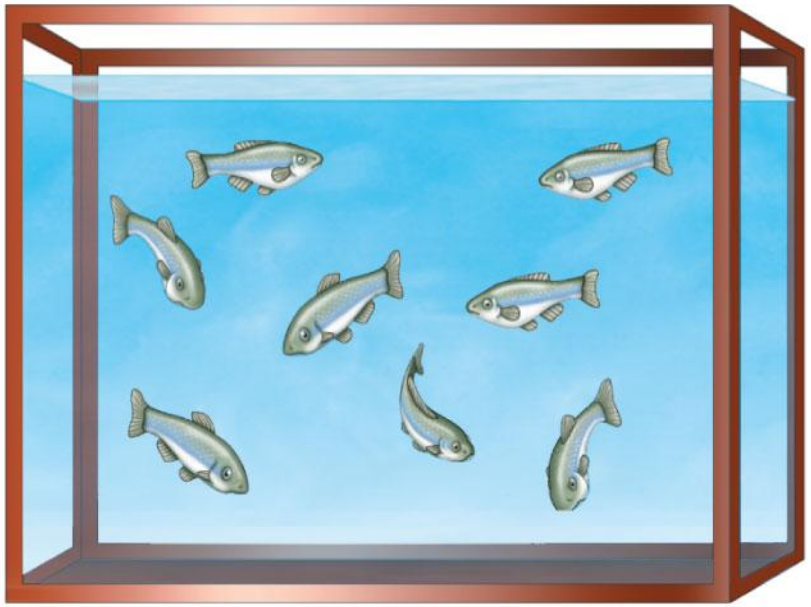
- produces pheromones
- affects the development and behavior of female workers and male drones

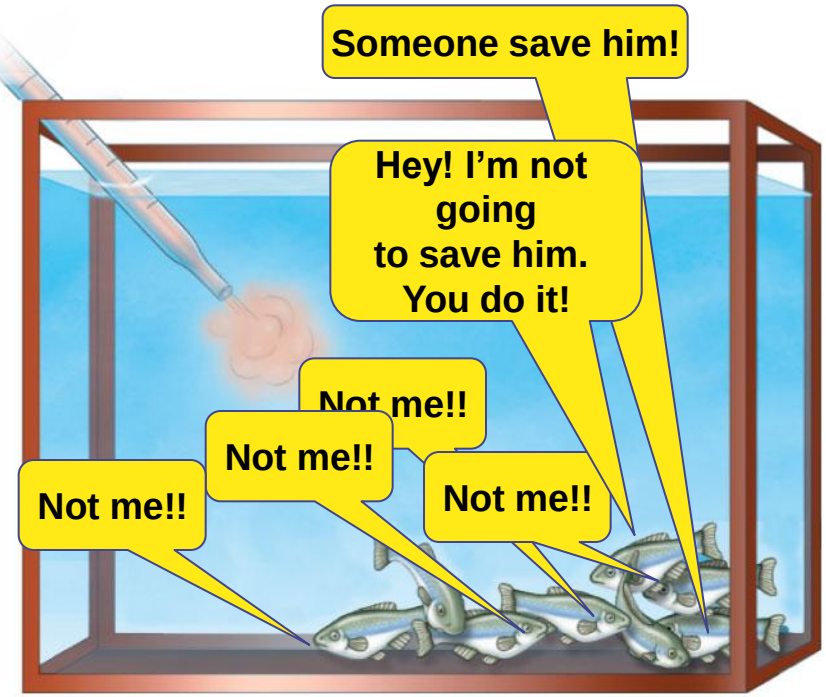


Location A | Location B | Location C

Pheromones

- Minnow or catfish is injured!
- Alarm substance in the fish's skin disperses in the water… This induces a fright response among the fish





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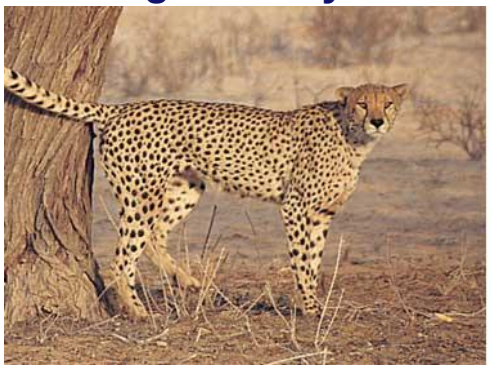
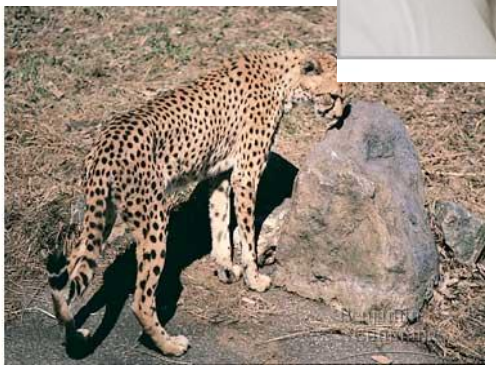
human sex pheromone?

Pheromones

Female mosquito use CO_2 concentrations to locate victims

marking territory



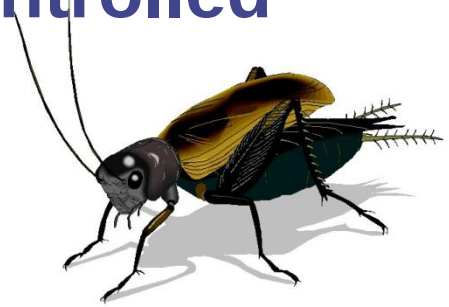


Spider using moth sex pheromones, as allomones, to lure its prey

The female lion lures male by spreading sex pheromones, but also by posture & movements

Communication by song

- **Bird song**
  - species identification & mating ritual
  - mixed learned & innate
  - critical learning period
- **Insect song**
  - mating ritual & song
  - innate, genetically controlled



Red-winged blackbird

Experience and Behavior

Cross-fostering studies

- identify role of environment to behavior
- places the young from one species in the care of adults from another species

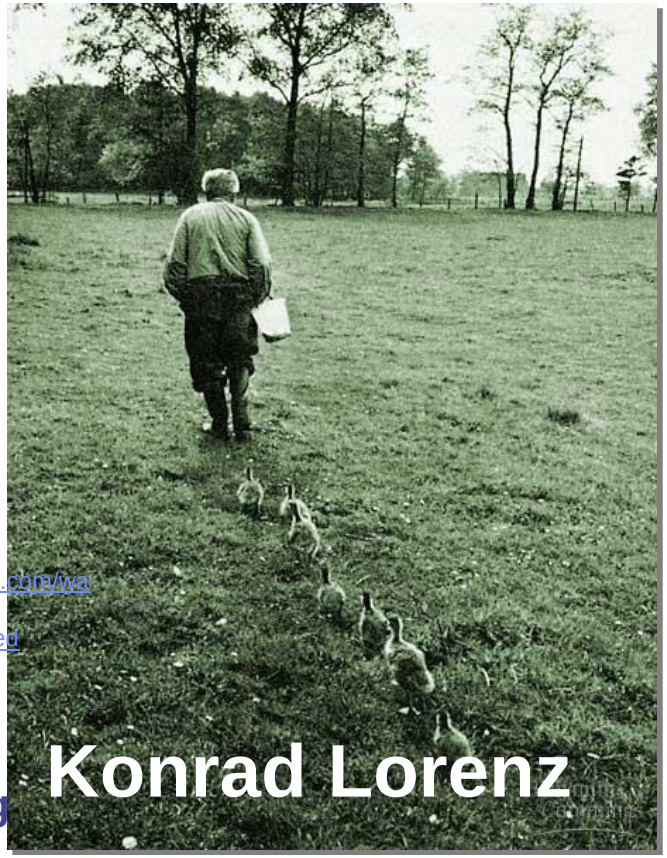
Table 51.1 Influence of Cross-Fostering on Male Mice*

Species	Aggression Toward an Intruder	Aggression in Neutral Situation	Paternal Behavior
California mice fostered by white-footed mice	Reduced	No difference **Innate**	Reduced
White-footed mice fostered by California mice	No difference **Innate**	Increased	No difference **Innate**

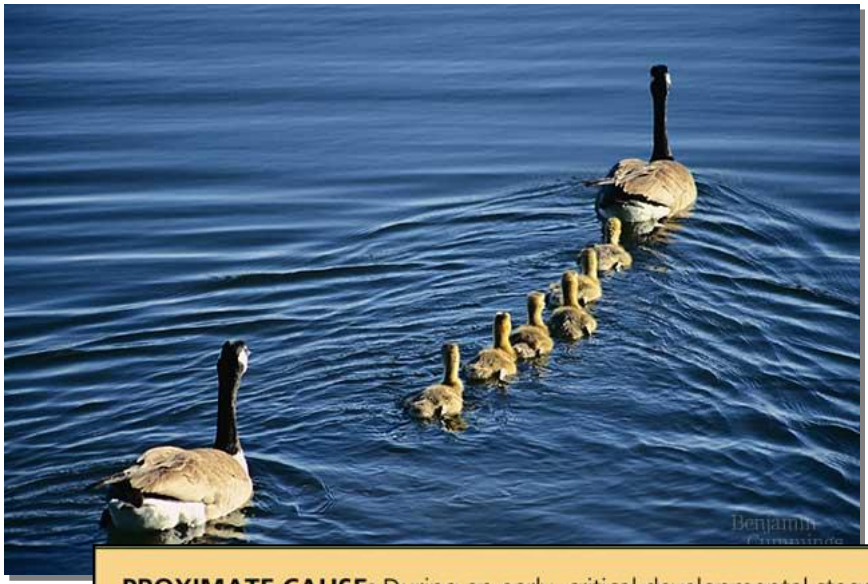
*Comparisons are with mice raised by parents of their own species.

Innate & Learning: Imprinting

- Learning to form social attachments at a specific critical period
  - both learning & innate components



http://www.youtube.com/watch?v=2UIU9XH-mUI&feature=related



PROXIMATE CAUSE: During an early, critical developmental stage, the young geese observe their mother moving away from them and calling.

ULTIMATE CAUSE: On average, geese that follow and imprint on their mother receive more care and learn necessary skills, and thus have a greater chance of surviving than those that do not follow their mother.

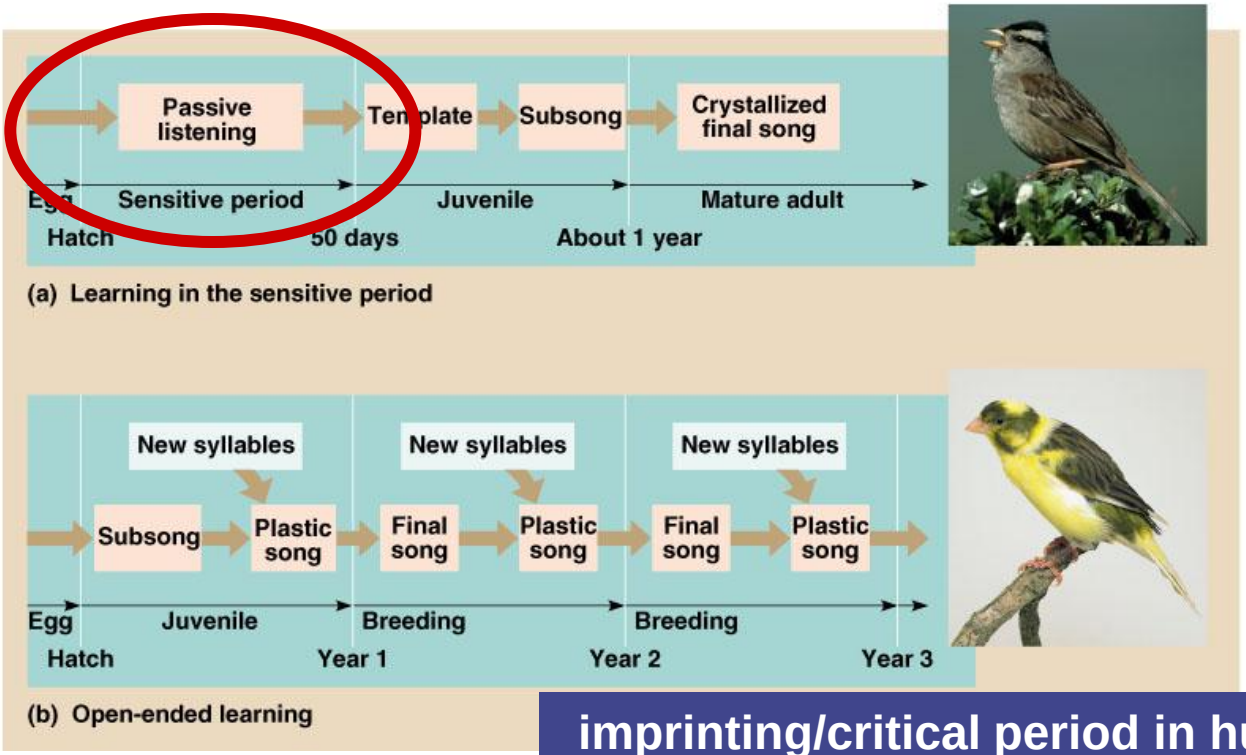
Conservation

Conservation biologists have taken advantage of imprinting by young whooping cranes as a means to teach the birds a migration route. A pilot wearing a crane suit in an Ultralight plane acts as a surrogate parent.

Critical period

- Sensitive phase for optimal imprinting
  - some behavior must be learned during a receptive time period

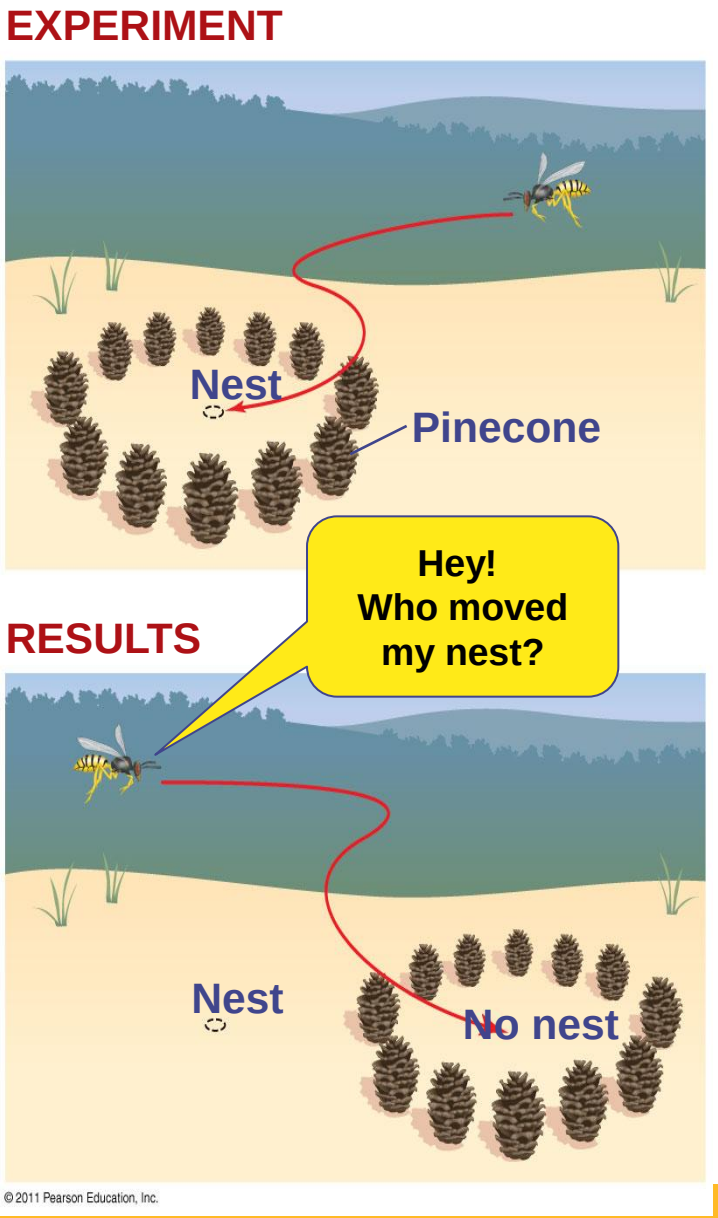
As a brood parasite, the Cuckoo never learn the song of their species as a nestling. Song development is totally innate.



imprinting/critical period in humans?

Spatial Learning and Cognitive Maps

- more complex modification of behavior
- based on experience with the spatial structure of the environment
- Niko Tinbergen- digger wasps use landmarks to find nest entrances
- A cognitive map- internal representation of spatial relationships between objects in an animal's surroundings



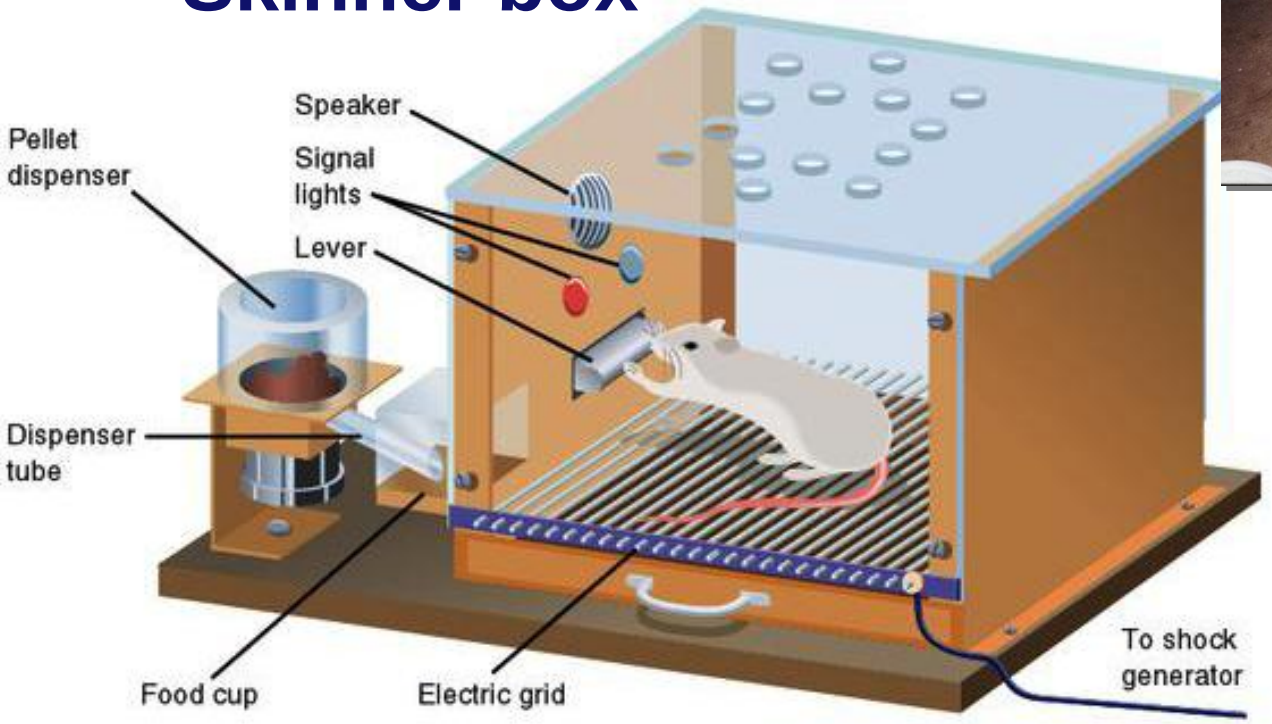
Learned behavior

- **Associative learning**
  - learning to associate a stimulus with a consequence
    - **operant conditioning**
      - trial & error learning
      - associate behavior with reward or punishment
      - ex: learning what to eat
    - **classical conditioning**
      - Pavlovian conditioning
      - associate a "neutral stimulus" with a "significant stimulus"

QuickTime™ and a
TIFF (Uncompressed) decompressor
are needed to see this picture.

Operant conditioning

- **Skinner box**



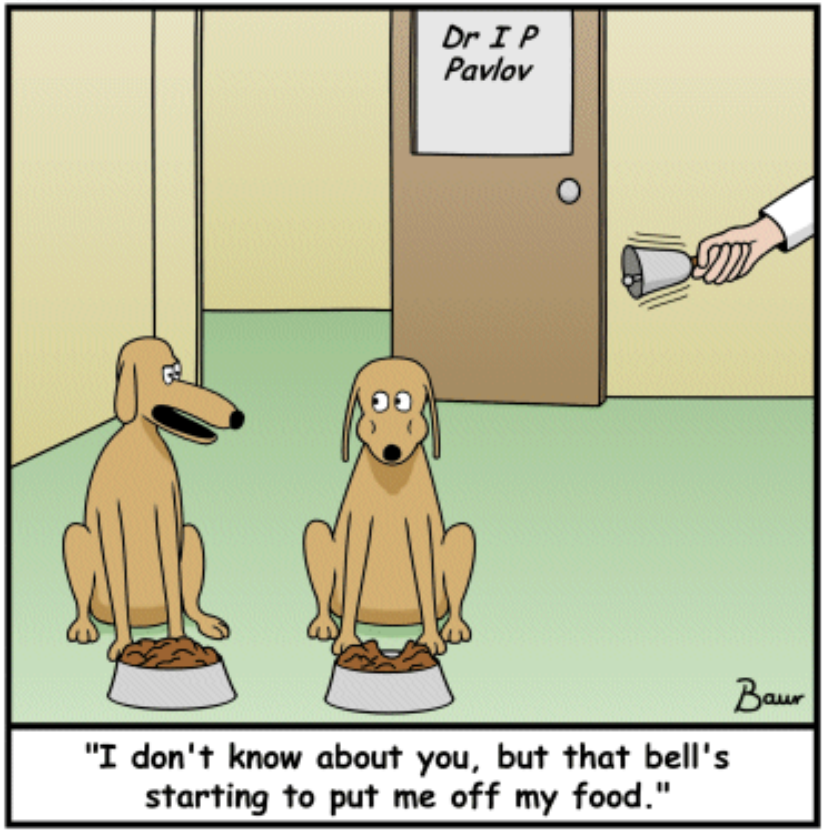
B. F. Skinner

QuickTime™ and a
TIFF (Uncompressed) decompressor
are needed to see this picture.

mouse learns to associate behavior (pressing lever) with reward (food pellet)

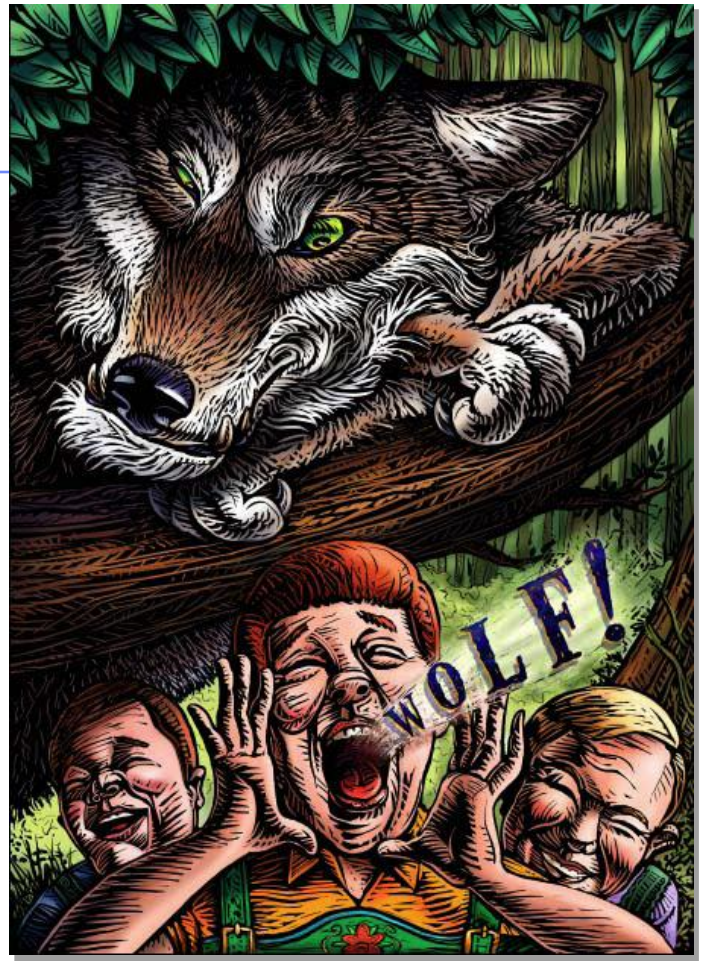
Classical conditioning

- **Ivan Pavlov's dogs**
  - **connect reflex behavior (salivating at sight of food) to associated stimulus (ringing bell)**



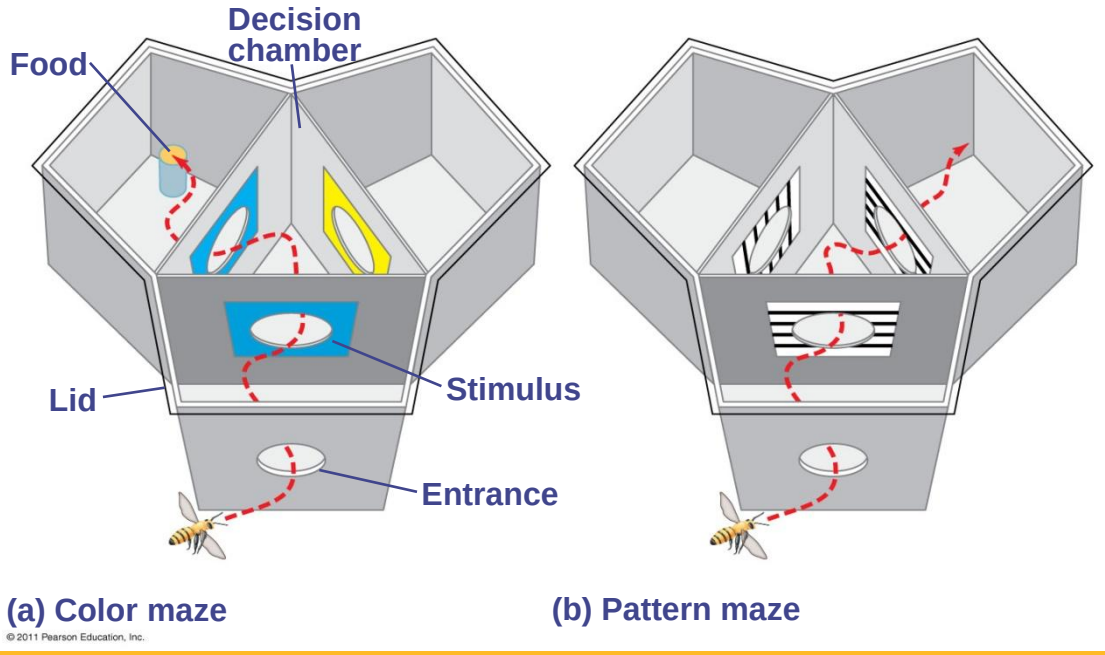
Learning: Habituation

- Loss of response to stimulus
  - “cry-wolf” effect
  - decrease in response to repeated occurrences of stimulus
  - enables animals to disregard unimportant stimuli
    - ex: falling leaves not triggering fear response in baby birds



Cognition and Problem Solving

- **Cognition - process of knowing that includes awareness, reasoning, recollection, and judgment**
  - **For example, honeybees can distinguish "same" from "different"**



Learning: Problem-solving

- Do other animals reason?

chimpanzee

problem-solving

crow

tool use

sea otter

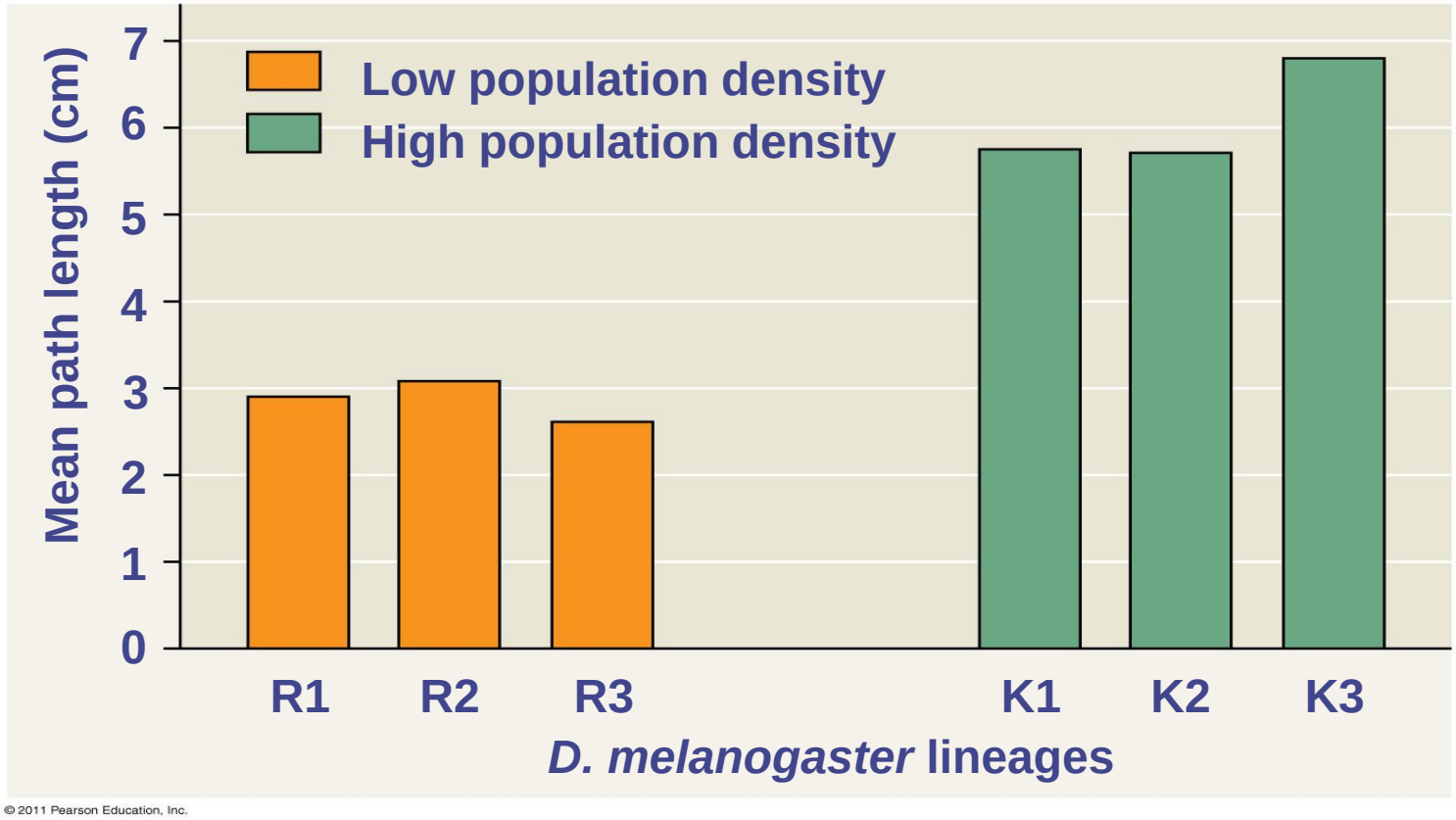
Social Learning

- learning by observing others
- forms the roots of culture
  - For example, young chimpanzees learn to crack palm nuts with stones by copying older chimpanzees
  - For example, vervet monkeys give and respond to distinct alarm calls for different predators

Foraging Behavior - *Food-gathering behavior*

- In *Drosophila*, gene variation dictates foraging behavior in the larvae
- Larvae with one allele forage farther than those with the other allele
- Larvae in high-density populations benefit from foraging farther for food
- Larvae in low-density populations benefit from short-distance foraging

- **Natural selection favors different alleles depending on the density of the population**



- **Under laboratory conditions, evolutionary changes in the frequency of these two alleles were observed over several generations**

Optimal Foraging Model

- A compromise between ***benefits of nutrition*** and ***costs of obtaining food***
- The costs of obtaining food:
  - energy expenditure
  - risk of injury/death

Prey- Mule deer are more likely to feed in open forested areas where they are less likely to be surprised, killed by mountain lions

Predators – select the old, weak, or young, not just because they are easier kills, but safer kills as well.

Mating Behavior and Mate Choice

- seeking or attracting mates
- choosing among potential mates,
- competing for mates
- caring for offspring

- Mating relationships define a number of distinct mating systems

Mating Systems and Sexual Dimorphism

Depending on the species….

- **Mating is promiscuous, with no strong pair-bonds or lasting relationships**

  Mating is based on monogamous relationships, one male mates with one female

- **Males and females with *monogamous mating systems* have similar external morphologies (look alike)**

(a) Monogamous species

(a) Monogamous species

(b) Polygynous species

(c) Polyandrous species

Polygamous relationships

- In *polygamous relationships*, an individual of one sex mates with several individuals of the other sex
- Species with polygamous mating systems are *usually sexually dimorphic:* males and females have different external morphologies
- Antlers/no antlers, size difference, etc.
- Polygamous relationships can be either polygynous or polyandrous

- In ***polygyny***, one male mates with many females.
- The males are usually more showy and larger than the females. Also, the greater the size differential, the greater the number of female mates.

(b) Polygynous species

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- In ***polyandry***, one female mates with many males
- The females are often more showy than the males

(c) Polyandrous species

Mating Systems and Parental Care

- Needs of the young are an important factor constraining evolution of mating systems

- **Consider bird species where chicks need a continuous supply of food**
- **What is the male's best strategy?**
  - **A male maximizes his reproductive success by staying with his mate and caring for his chicks (*monogamy*)**
- **Consider bird species where chicks are soon able to feed and care for themselves**
  - **A male maximizes his reproductive success by seeking additional mates (*polygyny*)**

- ***Certainty of paternity*** **influences parental care and mating behavior**
- **Females can be certain that eggs laid or young born contain her genes; however, paternal certainty depends on mating behavior**
- **Paternal certainty is relatively low in species with internal fertilization because mating and birth are separated over time**

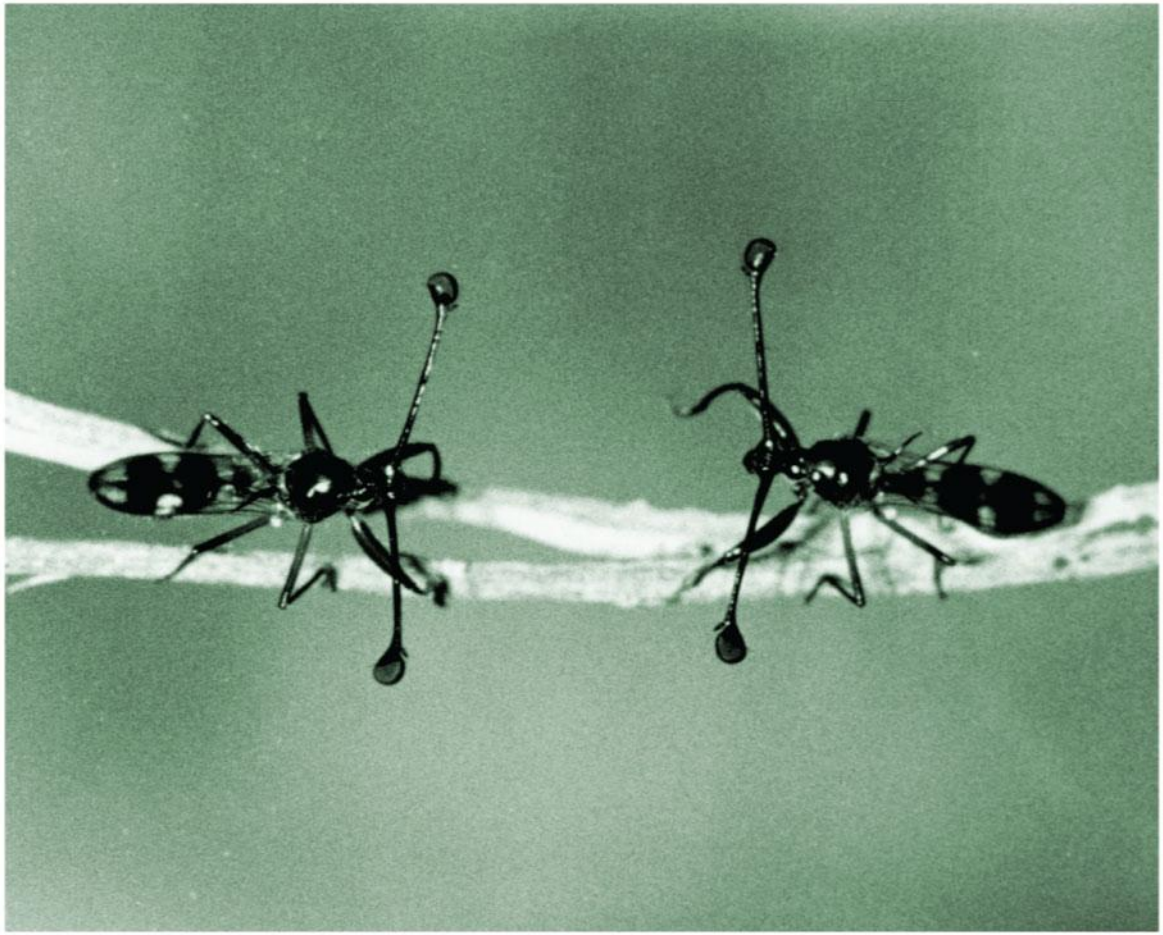
- Certainty of paternity is much higher when egg laying and mating occur together, as in external fertilization
- In species with external fertilization, parental care is at least as likely to be by males as by females

Sexual Selection and Mate Choice

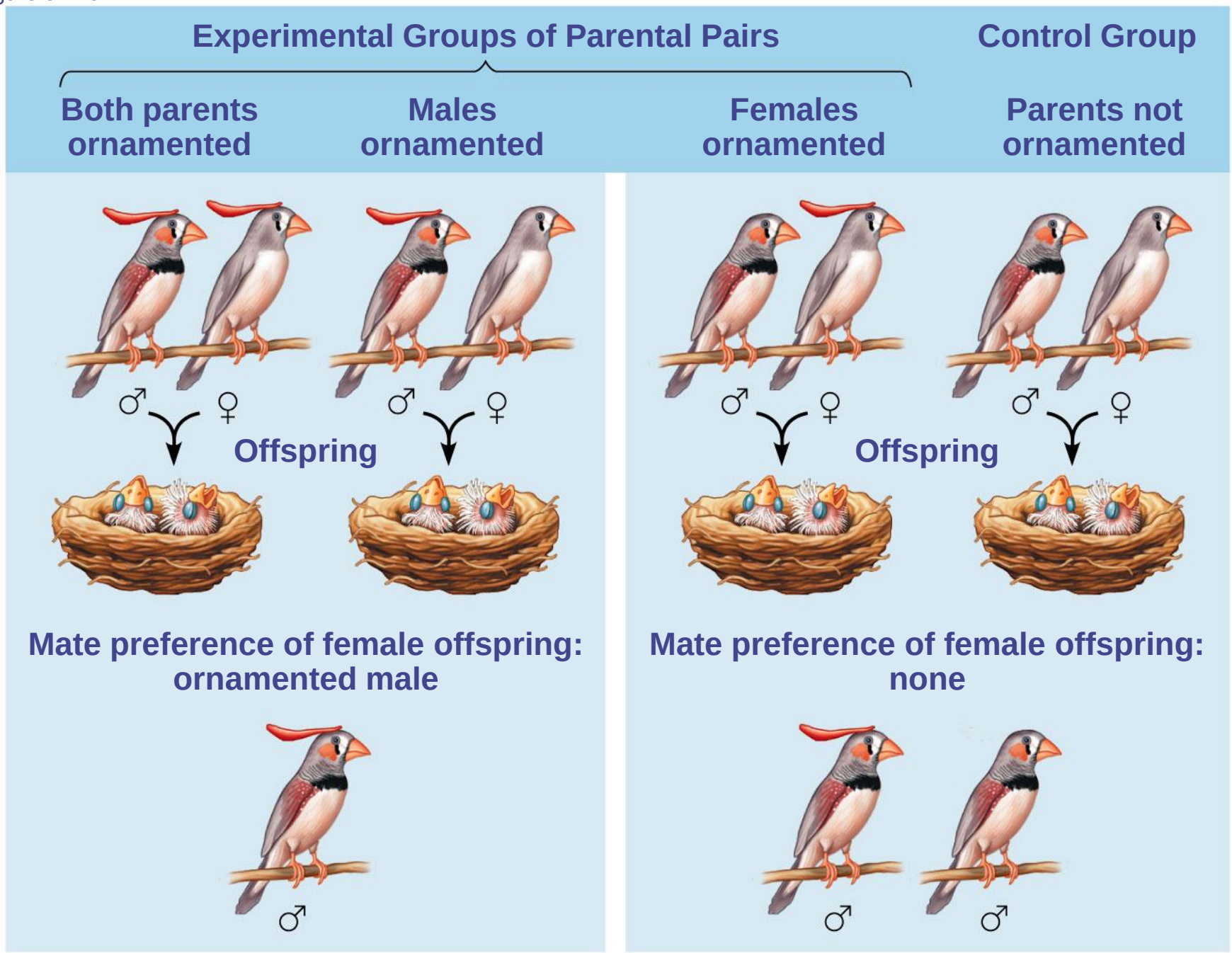
- ***Sexual dimorphism*** **results from sexual selection, a form of natural selection**
- **In *intersexual selection*, members of one sex choose mates on the basis of certain traits**
- ***Intrasexual selection*** **involves competition between members of the same sex for mates**

Mate Choice by Females

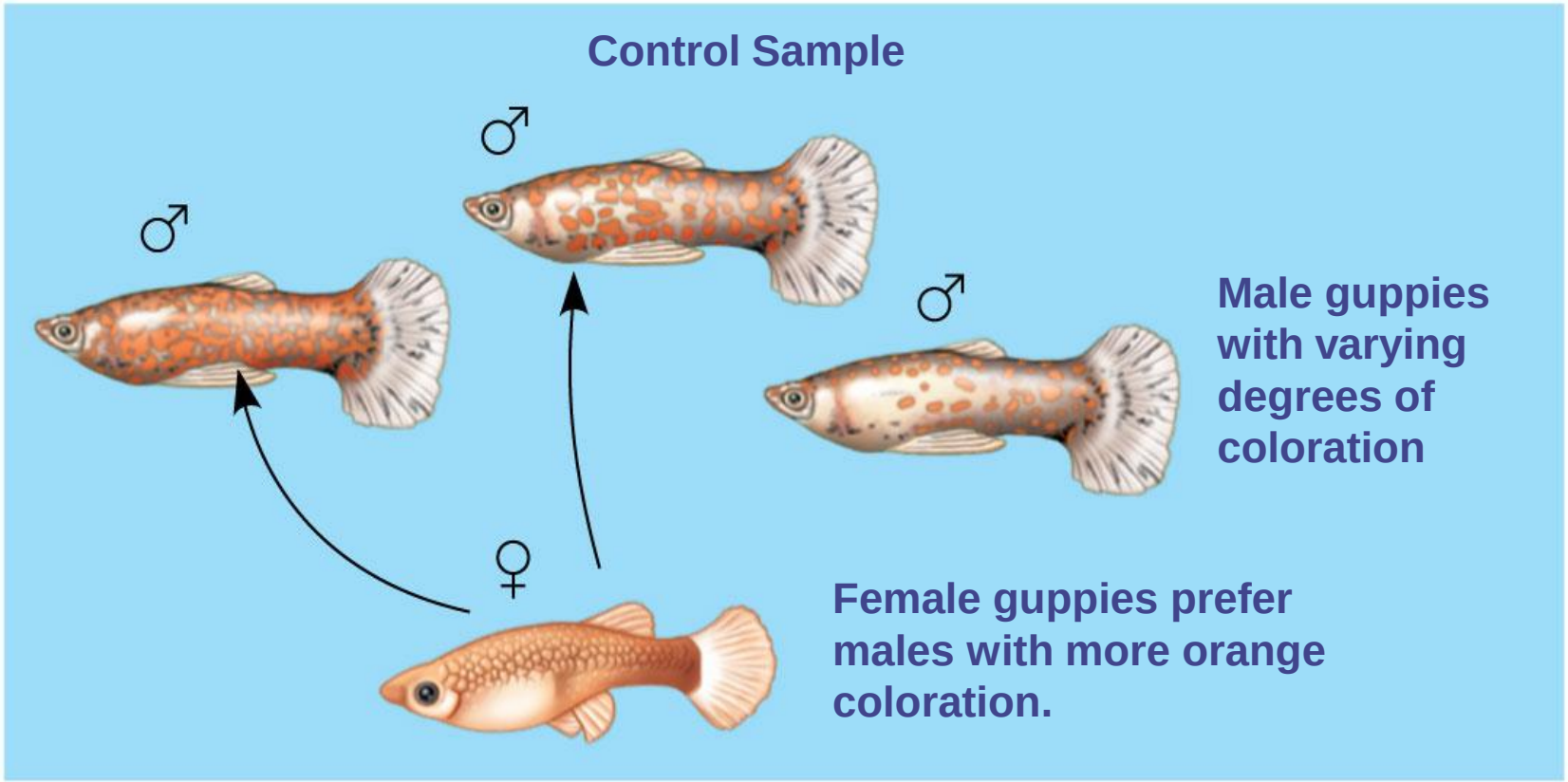
- **Female choice is a type of intersexual competition**
- **Females can driv**
  males with specif
  anatomy
  - **For example, f**
    males with rela
- **Ornaments, such**
  correlate with hea

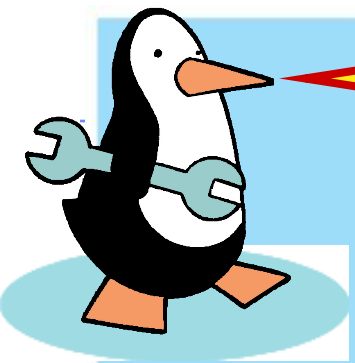


- Another example of mate choice by females occurs in zebra finches
- ***Female chicks who imprint on ornamented fathers are more likely to select ornamented mates***
- Experiments suggest that mate choice by female zebra finches has played a key role in the evolution of ornamentation in male zebra finches

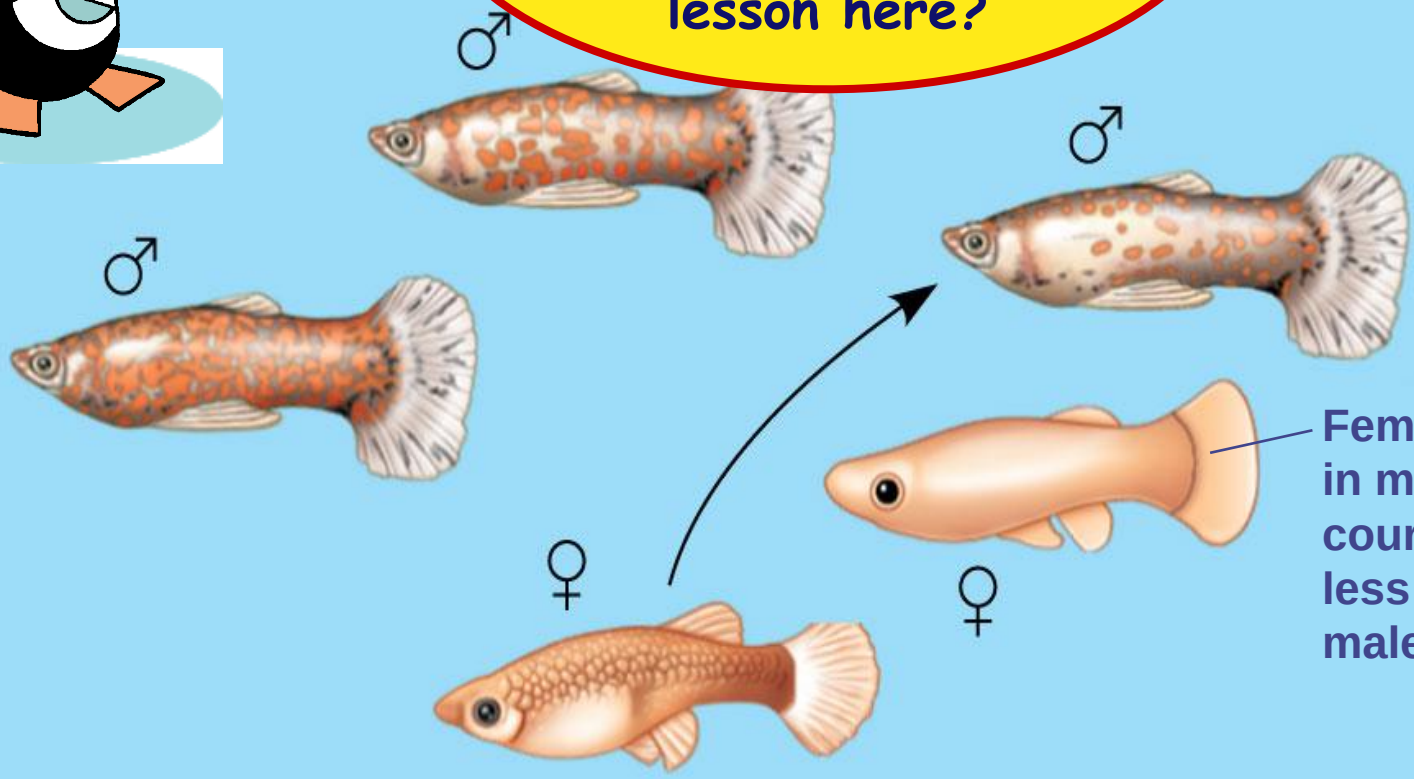


- **Mate-choice copying is a behavior in which individuals copy the mate choice of others**
  - **For example, in an experiment with guppies, the choice of female models influenced the choice of other females**





Guys! Here is where scientific research can pay off personally! What is the lesson here?



Female model in mock courtship with less orange male

Female guppies prefer males that are associated with another female.

Male Competition for Mates

- Male competition for mates is a source of intrasexual selection that can reduce variation among males
- Such competition may involve agonistic behavior, an often ritualized contest that determines which competitor gains access to a resource

Applying Game Theory

- The evolution of *alternative* mating behavior and morphology in males
- Game theory evaluates alternative strategies where the outcome depends on each individual's strategy and the strategy of other individuals

Male side-blotched lizards have a yellow, blue, or orange throat

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- **Each color is associated with a specific strategy for obtaining mates**
  - **Orange-throat males** - most aggressive and defend large territories
  - **Blue-throats** defend small territories
  - **Yellow-throats** are non-territorial, *mimic females*, and use "sneaky" strategies to mate

- Like rock-paper-scissors
- each strategy will outcompete one strategy but be outcompeted by the other strategy
- The success of each strategy depends on the frequency of all of the strategies; this drives ***frequency-dependent selection***

Altruism

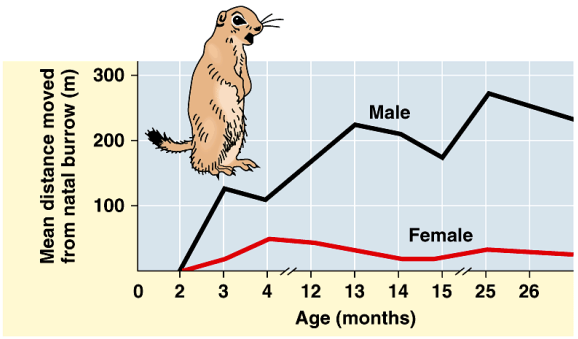
- Natural selection favors behavior that maximizes an individual's survival and reproduction
- These behaviors are often selfish
- On occasion, some animals behave in ways that reduce their individual fitness but increase the fitness of others
- This kind of behavior is called ***altruism***, or selflessness

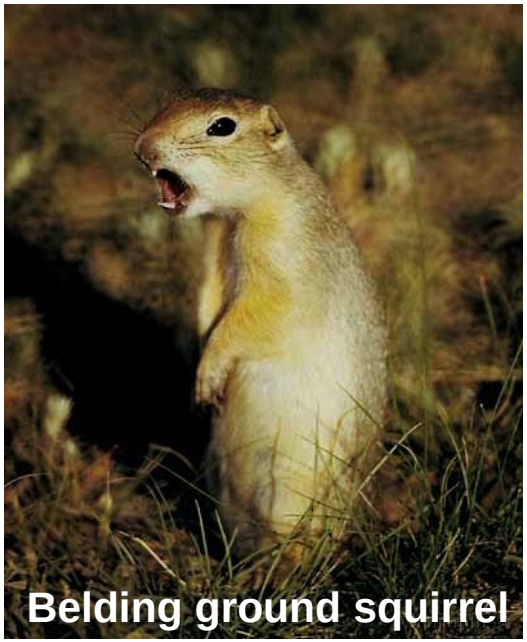
Inclusive Fitness

- Altruism can be explained by ***inclusive fitness***
- Inclusive fitness is the total effect an individual has on proliferating its genes by producing offspring and helping close relatives produce offspring

Social behaviors

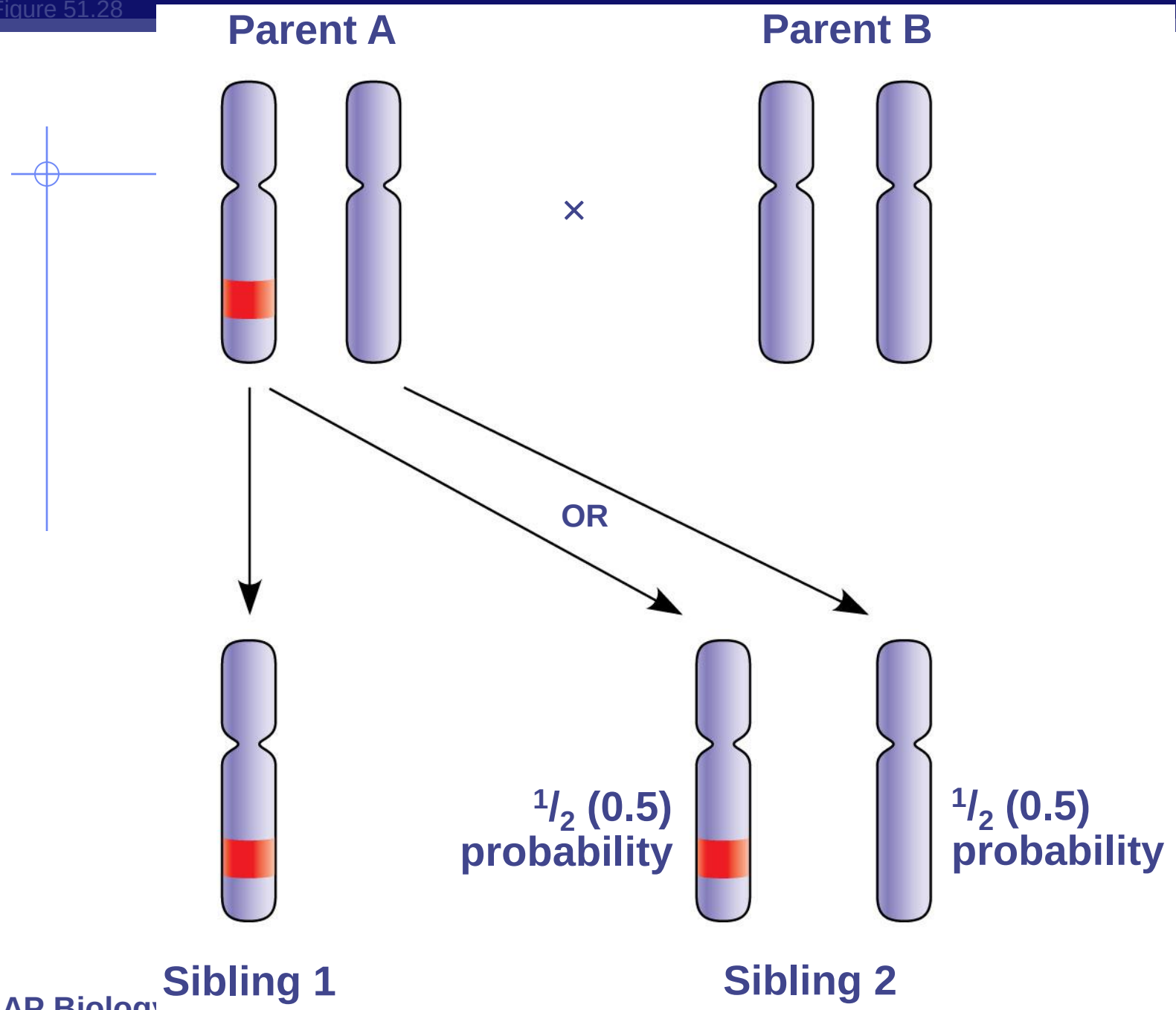
- **Altruistic behavior**
  - reduces individual fitness but increases fitness of recipient
  - **kin selection**
    - increasing survival of close relatives passes these genes on to the next generation





Hamilton's Rule and Kin Selection

- William Hamilton proposed a quantitative measure for predicting when natural selection would favor altruistic acts among related individuals
- Three key variables in an altruistic act
  - Benefit to the recipient (*B*)
  - Cost to the altruistic (*C*)
  - Coefficient of relatedness (the fraction of genes that, on average, are shared; *r*)



- **Natural selection favors altruism when**

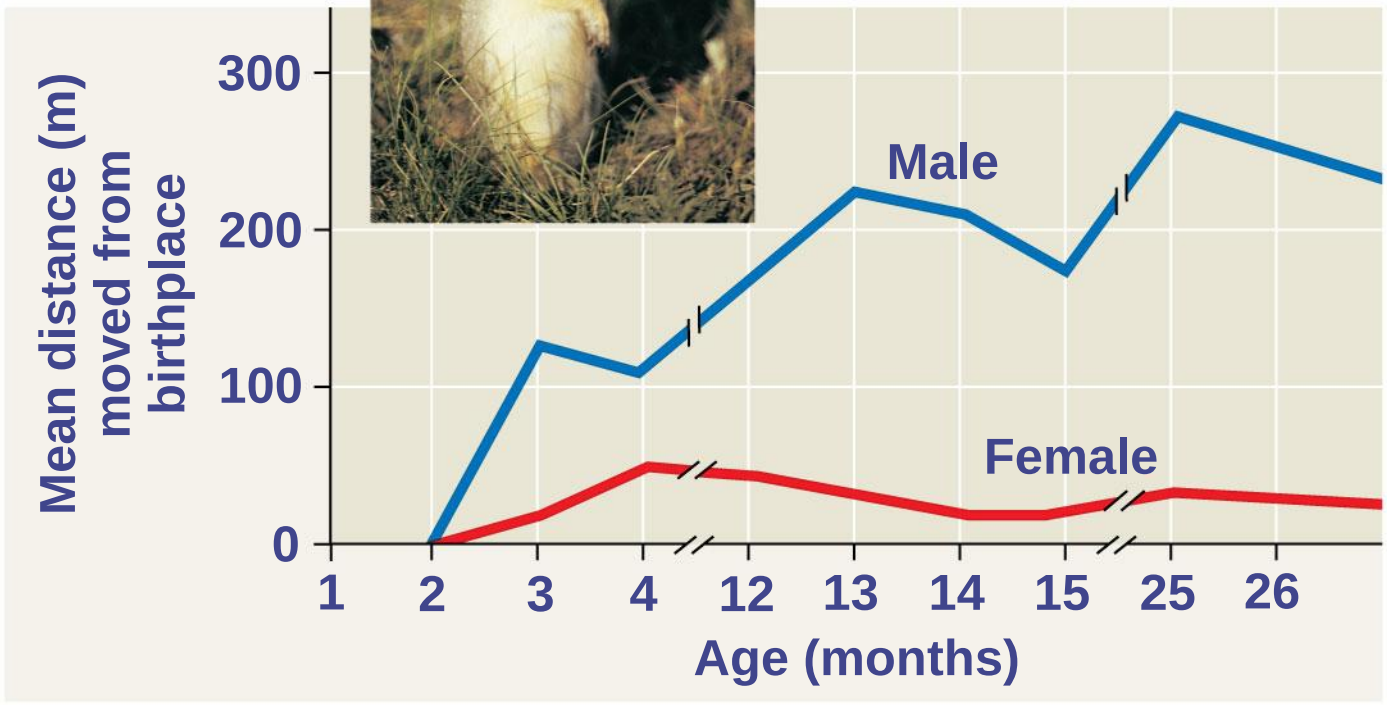
$$rB > C$$

Coefficient of relatedness x Benefit to the recipient (*B*) >Cost to the altruistic (*C*)

- **This inequality is called *Hamilton's rule***
- **Hamilton's rule is illustrated with the following example of a girl who risks her life to save her brother**

- **Assume the average individual has two children. As a result of the sister's action:**
  - The brother can now father two children, so $B = 2$
  - The sister has a 25% chance of dying and not being able to have two children, so $C = 0.25 \times 2 = 0.5$
  - The brother and sister share half their genes on average, so $r = 0.5$
- **If the sister saves her brother rB (= 1) > C (= 0.5)**

- ***Kin selection*** **- natural selection that favors altruistic behavior by *enhancing reproductive success of relatives***
- **An example of kin selection and altruism is the warning behavior in Belding's ground squirrels**
- **In a group, most of the females are closely related to each other**
- **Most alarm calls are given by females who are likely aiding close relatives**



Reciprocal Altruism

- Altruistic behavior toward unrelated individuals can be adaptive *if the aided individual returns the favor in the future*
- limited to species with stable social groups where individuals meet repeatedly, and *cheaters (who don't reciprocate) are punished!*

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- Reciprocal altruism has been used to explain altruism between unrelated individuals in humans

- ***Game Theory***: **A tit-for-tat strategy with the following rules:**
  - **Individuals always cooperate on first encounter**
  - **An individual treats another the same way it was treated the last time they met**
    - **That is, individuals will always cooperate, unless their opponent cheated them the last time they met**

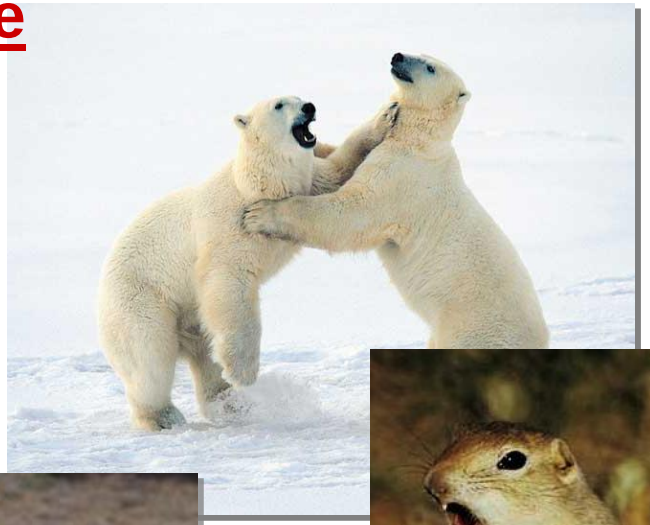
Individuals who engage in a tit-for-tat strategy have *a higher fitness than individuals* who are always selfish!

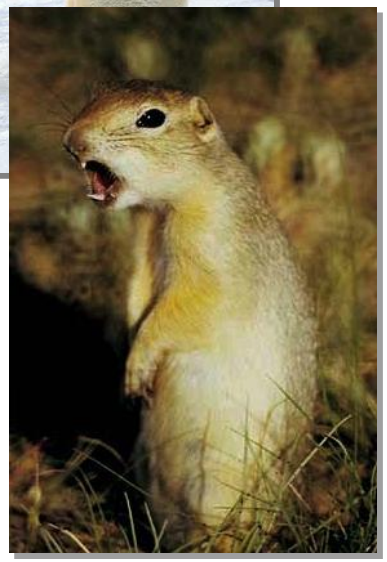
Any Questions??

Ghosts of Lectures Past….

Social behaviors

- Interactions between individuals
  - develop as evolutionary adaptations
  - communication / language
  - agonistic behaviors
  - dominance hierarchy
  - cooperation
  - altruistic behavior





Social behaviors

- **Agonistic behaviors**
  - threatening & submissive rituals
    - symbolic, usually no harm done
  - ex: territoriality, competitor aggression

Social behaviors

- **Dominance hierarchy**
  - social ranking within a group
    - pecking order

Social behaviors

- **Cooperation**
  - working together in coordination

Pack of African dogs hunting wildebeest cooperatively

White pelicans “herding” school of fish