Chapter 51

Behavioral Ecology

What is behavior & why study it?

- **Behavior**
  - Everything an animal does & how it does it
    - Includes muscular and nonmuscular activity
    - Link between an animal & its environment
  - **Innate** = inherited or developmentally fixed
  - **Learned** = develop during animal's lifetime
- **Why study behavior?**
  - Part of phenotype
  - Acted upon by natural selection
    - May lead to greater fitness, reproductive success, survival

Behavior results from both genes & environment

- **Behaviors are phenotypes!**
- **Nature vs. nurture issue is not either/or**
- **Biologists ask how different factors influence behavior**
  - **Some behaviors are associated with specific genes ("sitter" vs. "rover" fruit flies)**
  - **Most behavioral traits are polygenic with environmental variables producing broad norms of reaction**

Genetic & environmental components of behavior

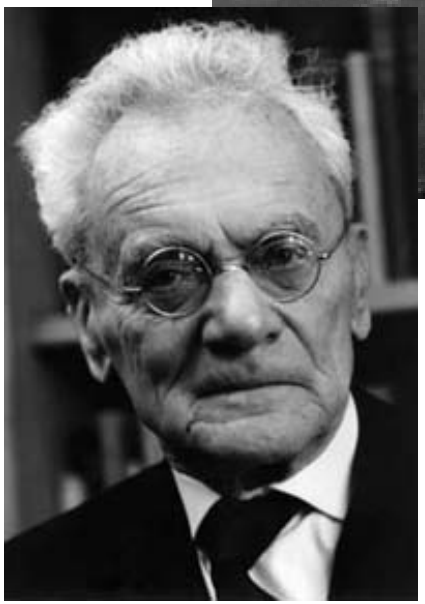
- **Ex. Lovebird nest-making behavior (Fig 51.1)**
  - **Fischer's lovebird makes 1 long paper strip & carries in beak**
  - **Peach-faced lovebird makes many short strips & carries in tail feathers (tucking behavior)**
  - **In first mating season, hybrid lovebird makes medium length strips & fails at tucking into tail feathers (resorts to carrying in beak)**
  - **Years later, birds still turn head (token tucking behavior) even though they carry strip in beaks**

Ethology

- **scientific study of animal behavior**
  - **particularly in natural environments**
  - **originated in the 1930s**
  - **defined a set of questions to guide research (proximate & ultimate causes)**

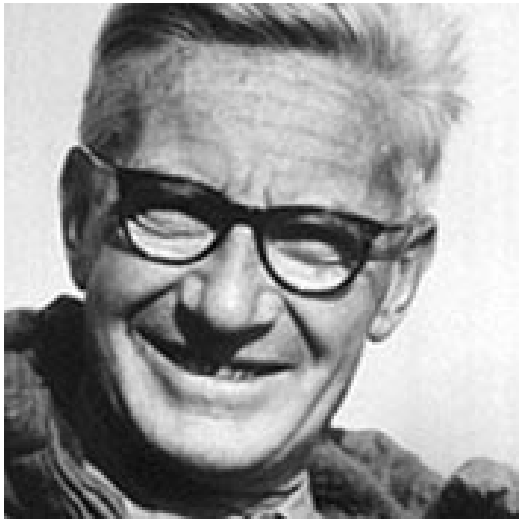
Pioneers in the study of animal behavior

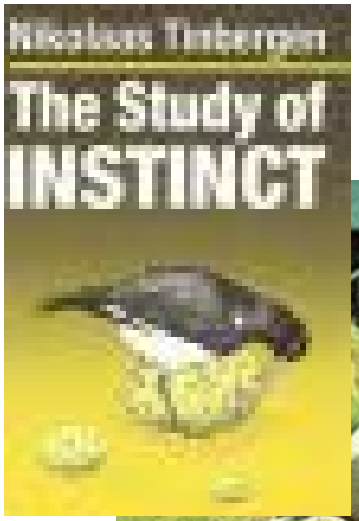
- **Karl von Frisch (1886-1982)**

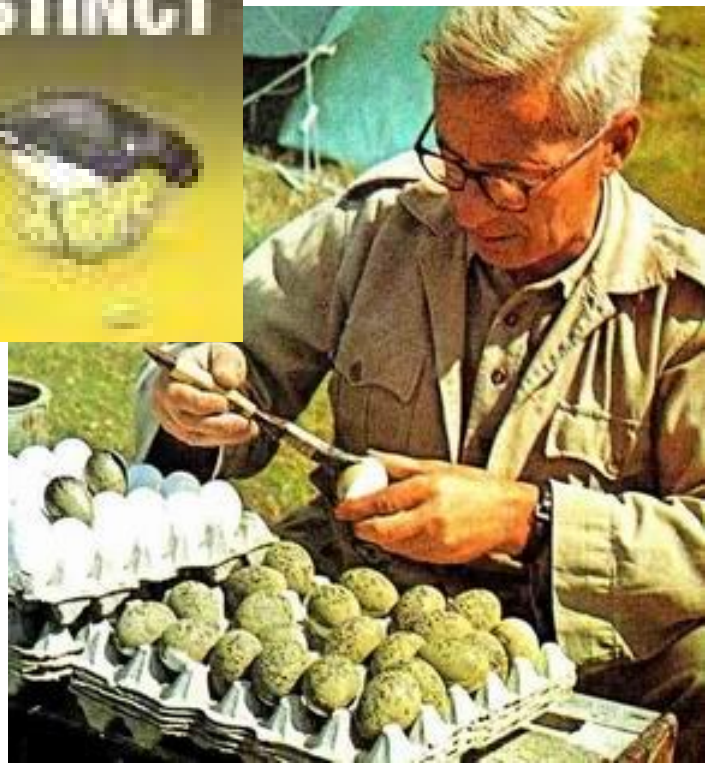


Pioneers in the study of animal behavior

- **Nikolaas “Niko” Tinbergen (1907-1988)**

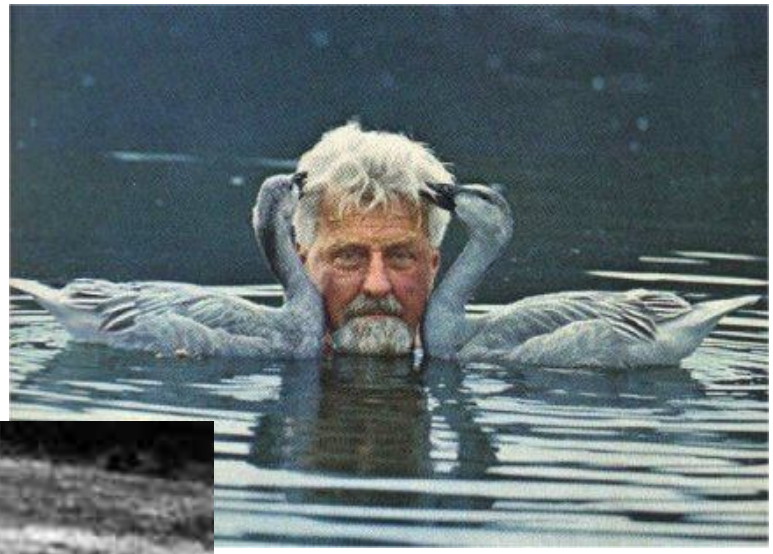






Pioneers in the study of animal behavior

- **Konrad Lorenz (1903-1989)**



What questions do we ask?

- **Proximate causes**
  - **Immediate stimulus & mechanism**
  - **“how” questions**
- **Ultimate causes**
  - **Evolutionary significance**
  - **How does behavior contribute to survival & reproduction**
  - **“why” questions**

Behavioral Ecology

- ***Evolution is the core theme of biology***
- **Behavioral ecology views behavior as an evolutionary adaptation to the natural ecological conditions of animals**
  - **Natural selection will favor behavioral patterns that enhance survival and reproductive success**
- **Evolutionary principles allow biologists to generate testable hypotheses to help explain behavior**

Experimental Evidence for Behavioral Evolution

- **Laboratory and field experiments can demonstrate the evolution of behavior**
- **Ex. cost-benefit analysis of foraging behavior**
  - **Foraging = all food-obtaining behavior & mechanisms used to recognize, search for, and capture food items**
  - **Optimal foraging theory – foraging behavior is a compromise between feeding costs & benefits**

cost-benefit analysis of foraging behavior

- **Crows in Pacific Northwest eat mollusks called whelks found in rocky tide pools**
  - **must drop whelks on rocks to break the shell**

- **Reto Zach of University of British Columbia conducted a cost-benefit analysis of foraging behavior of these crows**

cost-benefit analysis of foraging behavior

- **Optimal flight height = height resulting in least amount of work to break shell (fewest drops)**
- **Zach calculated & predicted optimal flight height based on shell drop experiments**
- **The observed average flight height for crows was very close to Zach's predicted height (~5 m)**

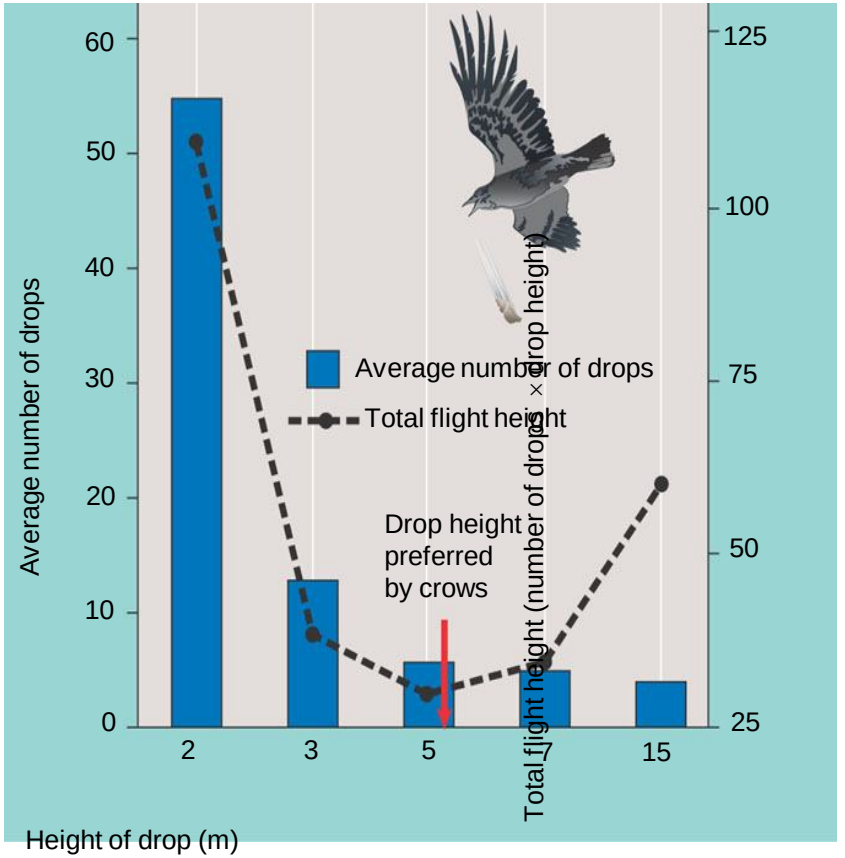
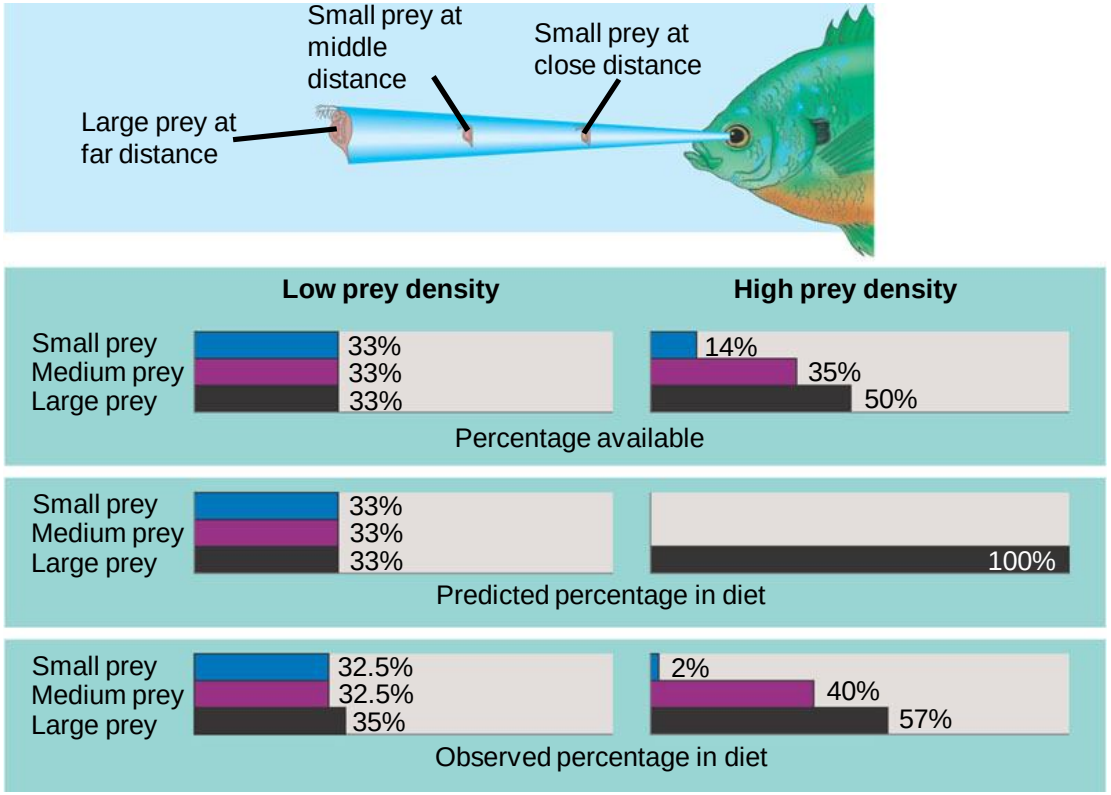


Figure 51.22

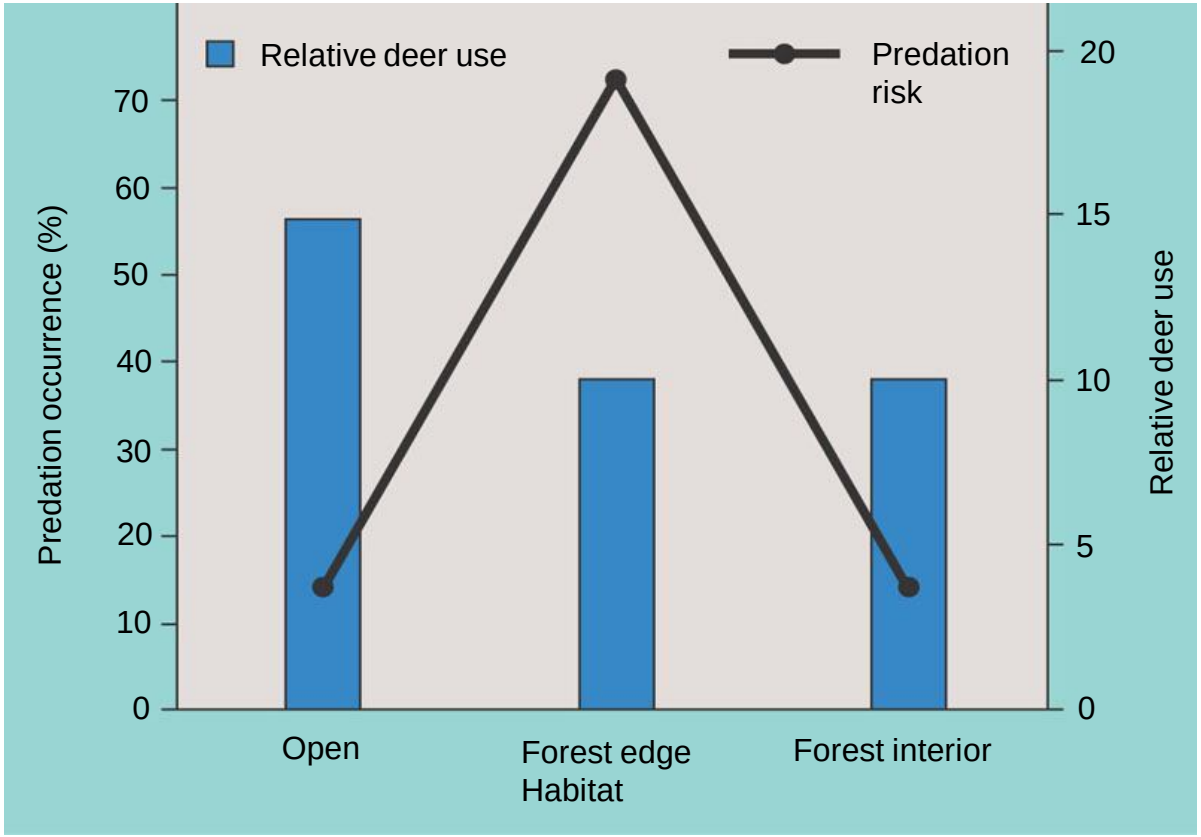
Foraging behavior & prey selection

- **Environment influences foraging behavior**
- **In bluegill sunfish prey selection behavior is related to prey density**



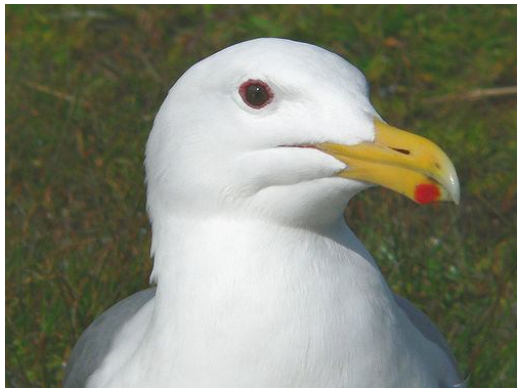
Foraging behavior & Risk of Predation

- **Research on mule deer populations has shown that predation risk affects where the deer choose to feed**



Types of behaviors

- **Innate behaviors**
  - Automatic, developmentally fixed; strong genetic influence
    - Despite different environments, all individuals exhibit the same behavior
    - Triggered by a stimulus



- **Learned behaviors**
  - Modified by experience
    - Variable
    - Triggered by a stimulus

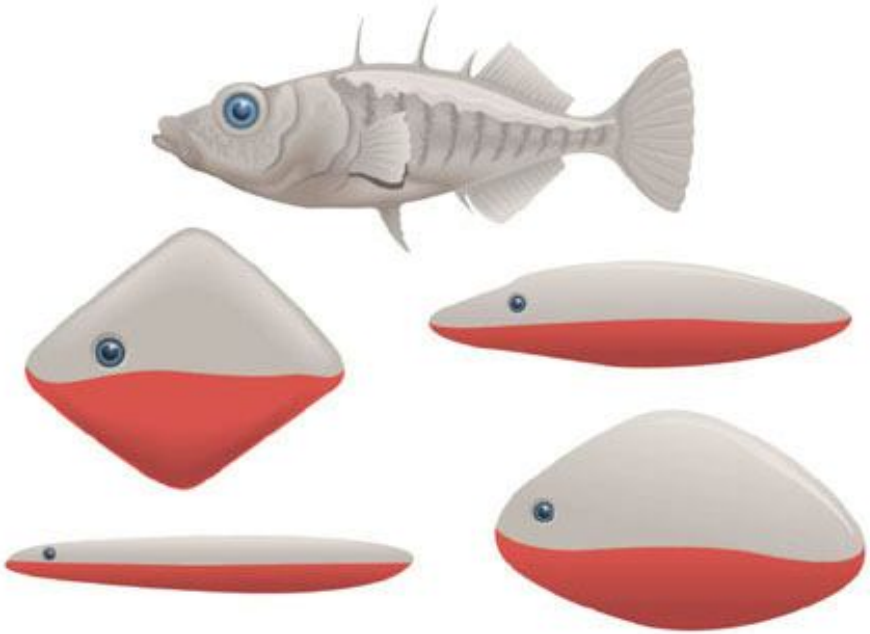
Innate behavior

- **Fixed action patterns (FAP)**
  - **Sequence of behaviors essentially unchangeable & usually conducted to completion once started**
  - **Triggered by sign stimulus (external sensory stimulus)**
    - **Key feature of animal's environment**
    - **Ex. some moths fold wings & drop to ground in response to ultrasonic bat signals**

Fixed action patterns

- **Male sticklebacks exhibit aggressive territoriality**
  - **Males have a red belly**

- **When presented with realistic & unrealistic models:**
  - **only attack models that have some red**
  - **ignore realistic model lacking red**



Fixed action patterns

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.

Sign stimulus

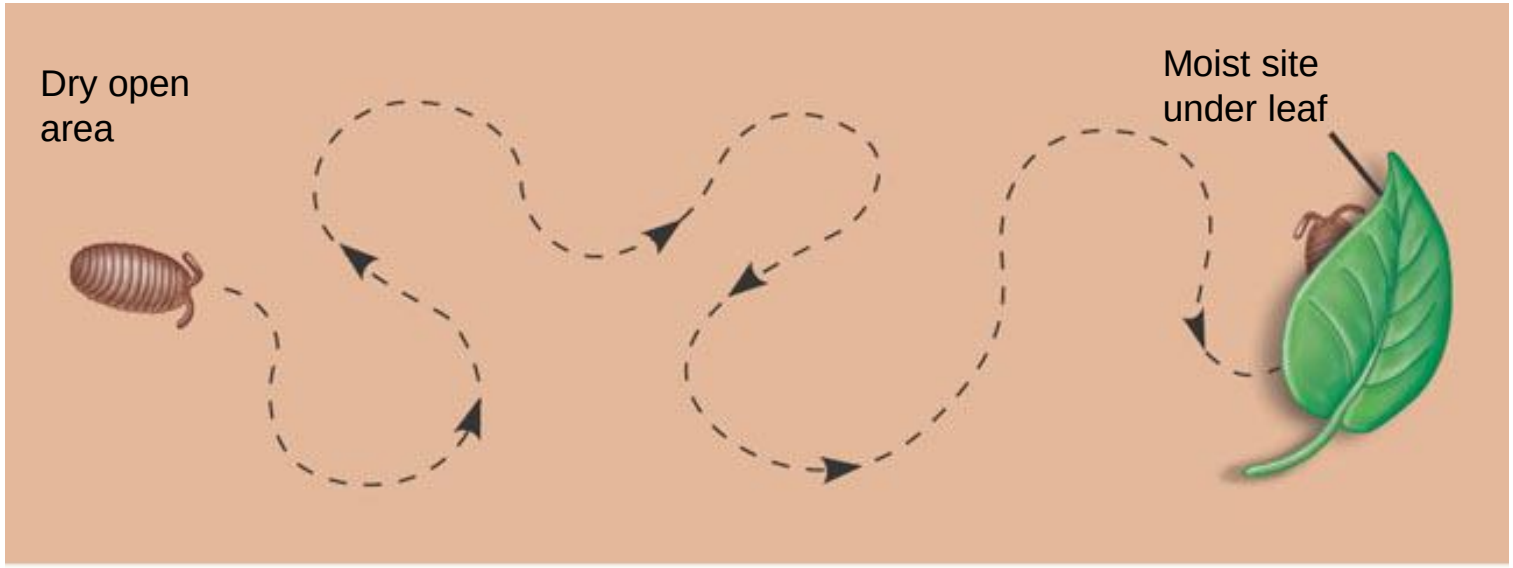
- **Animal responds to sign rather than to whole environment**
- **<u>Advantage</u>: faster appropriate response**
- **<u>Disadvantage</u>: animal can be tricked into inappropriate behavior**
  - **<u>Ex</u>. mayflies normally lay eggs on water, but may lay eggs on black plastic or asphalt instead (same light polarization)**

Directed Movements

- **Enable animals to:**
  - **avoid predators or poisons**
  - **migrate to a more favorable environment**
  - **obtain food**
  - **find mates & nest sites**
- **Three major kinds of directed movement (based on increasing cognitive complexity)**
  - **Kinesis & taxis**
  - **Use of landmarks**
  - **Cognitive maps**

Kinesis & taxis

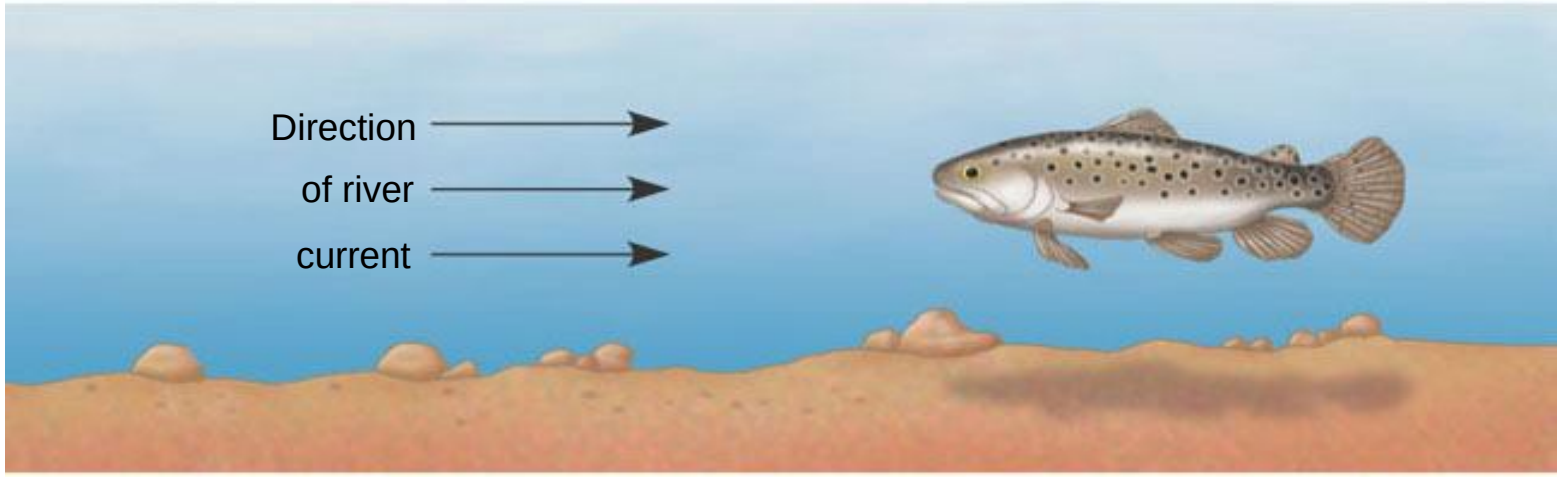
- **Kinesis – a simple change in activity or turning rate in response to a stimulus**
- **Ex: Sow bugs (isopods) become more active in dry areas and less active in humid areas**



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

Kinesis & taxis

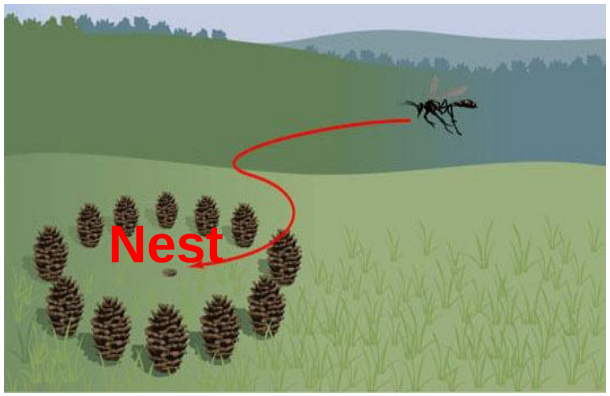
- **Taxis – a more or less automatic, oriented movement toward (positive taxis) or away from (negative taxis) a stimulus**
- **Ex: Many stream fish exhibit positive rheotaxis where they automatically swim in an upstream direction**

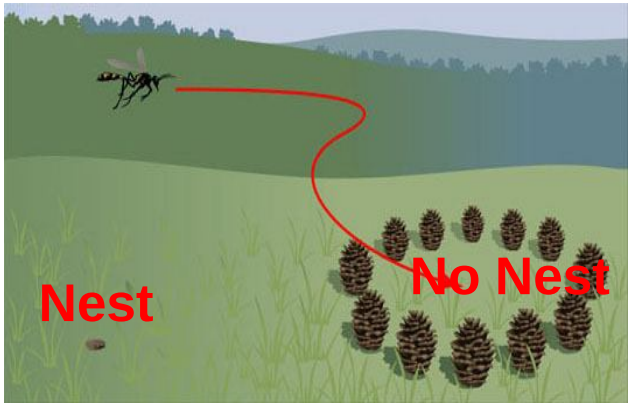


Positive rheotaxis keeps trout facing into the current, the direction from which most food comes.

Use of landmarks

- more complex cognitive mechanism
- stimulus is an arbitrary landmark that animal must learn
- Ex. Tinbergen's experiments with digger wasps





Female wasp used circle of pinecones to find her nest

Cognitive maps

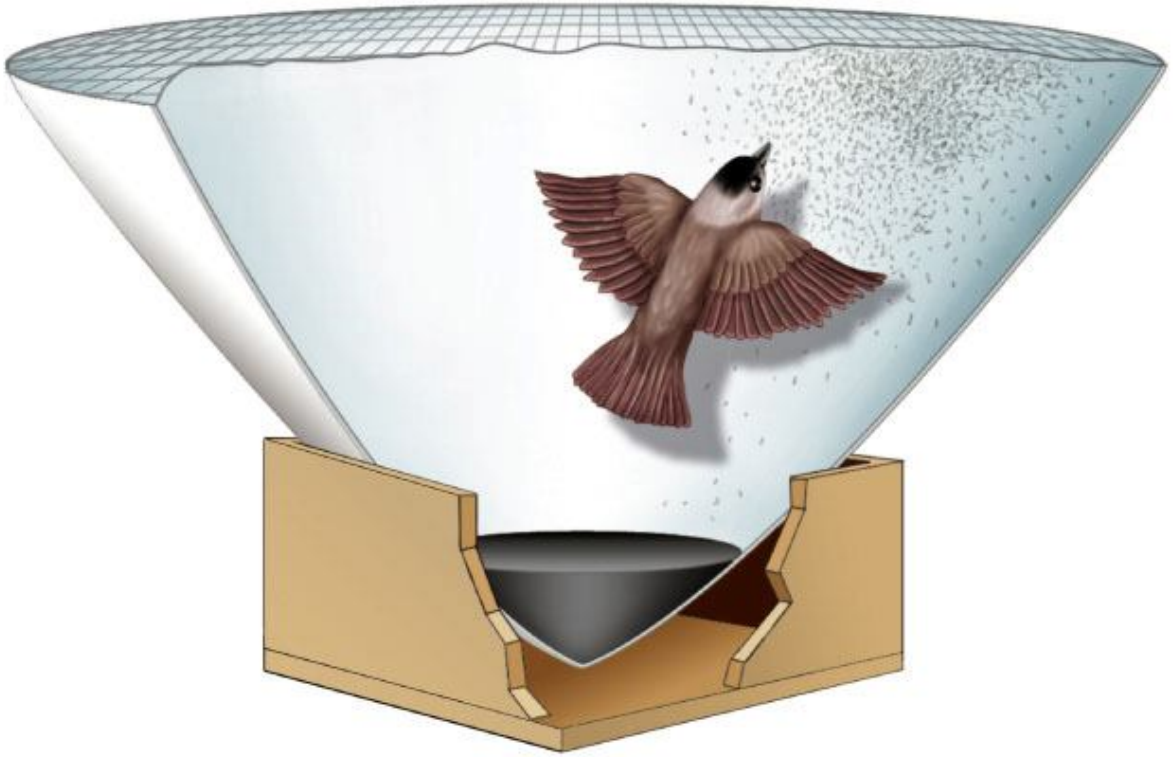
- **Internal representation, or code, of the spatial relationships among objects in an animal's surroundings**
  - **More powerful cognitive mechanism**
  - **Difficult to test; hard to tell if animal is using landmarks or cognitive map**
  - **Ex. jay stores food in thousands of caches; can relocate each one and keep track of food quality in each (bypasses caches containing perishable food)**

Migration

- **Regular movement over relatively long distances**
- **Complex behavior, but still under genetic control**

Genetic component of migration behavior

- **Ex: laboratory studies of migration behavior in blackcaps**
  - **Birds placed in funnel cages left marks indicating the direction they were trying to migrate**

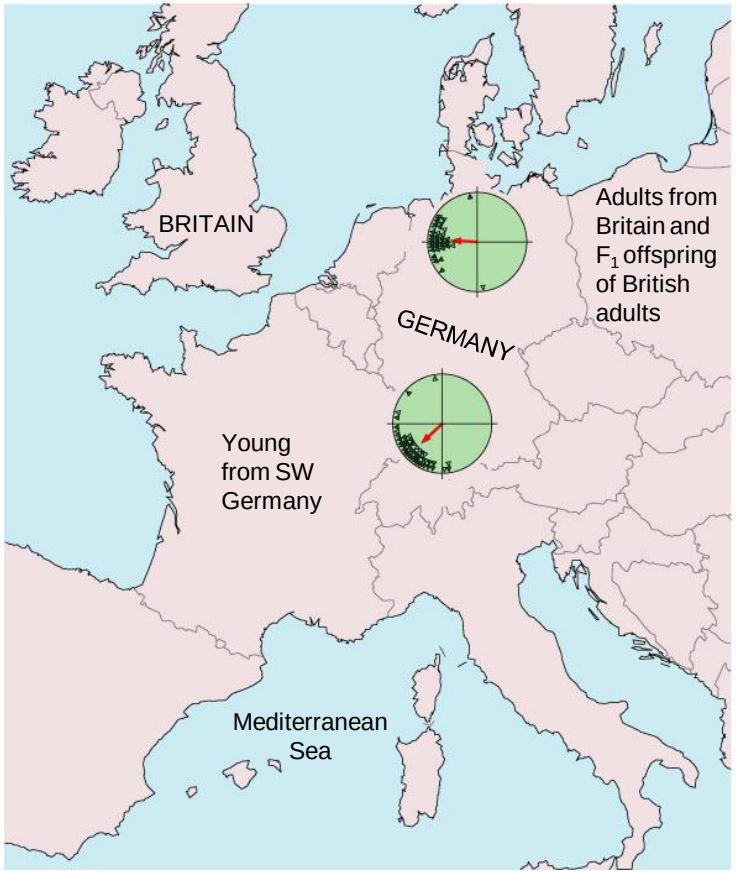


Genetic component of migration behavior

- **Migratory orientation of wintering adult birds captured in Britain was very similar to that of laboratory-raised birds**

  - **wintering blackcaps captured in Britain and their laboratory-raised offspring had a migratory orientation toward the west**

  - **young birds from Germany were oriented toward the southwest.**

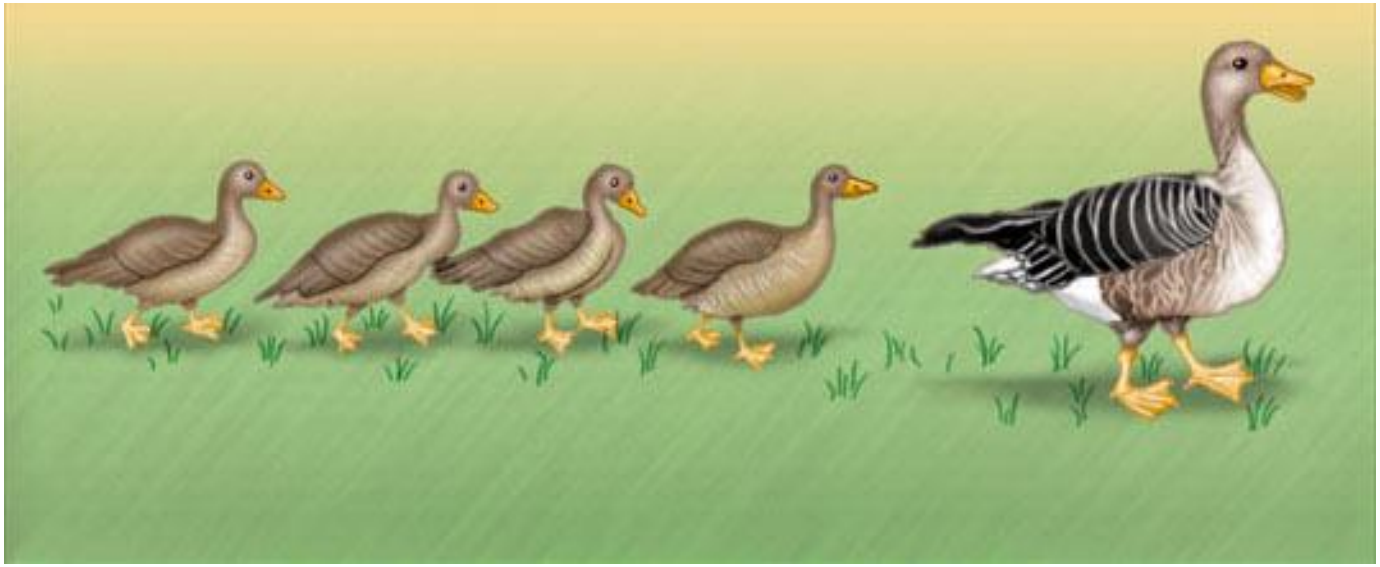


Imprinting

- **Learning that is limited to a specific critical time period (sensitive period)**
  - **forms social attachments**
  - **both learning and innate components**
  - **generally irreversible**
  - **Konrad Lorenz was "mother" to imprinted geese**

Imprinting

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.

Imprinting

- Conservation biologists have taken advantage of imprinting in programs to save the whooping crane from extinction

Associative learning

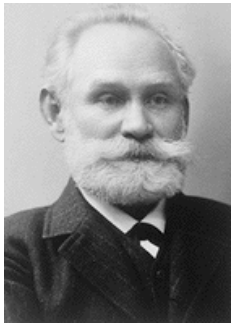
- **Learning to associate 1 feature of the environment (stimulus) with another**
    - **Operant conditioning (trial & error learning)**
    - **Classical conditioning (arbitrary stimulus & reward/punishment)**

Operant conditioning

- animal learns to associate one of its behaviors with a reward or punishment

Classical conditioning

- An **arbitrary stimulus** is associated with a reward or punishment



- Ex: Pavlov's dogs
  - Connect reflex behavior to conditioned response (salivating when bell rings)

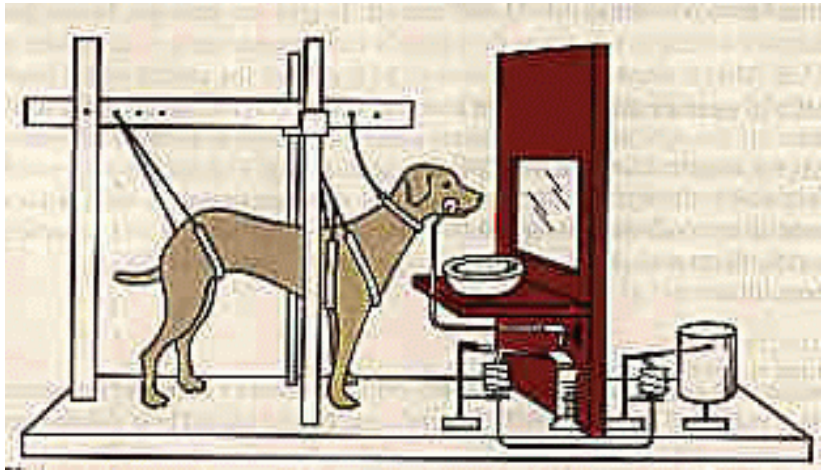
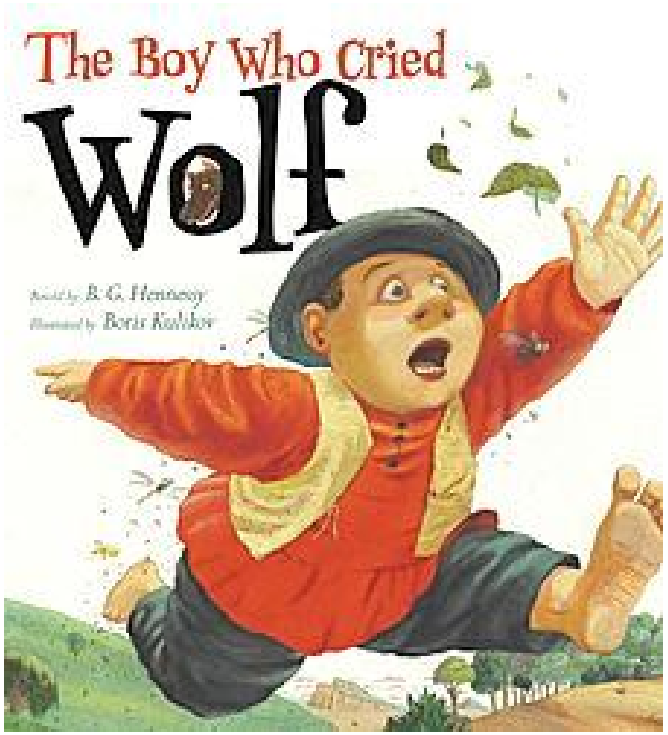


Figure 51.15

Habituation

- **loss of response to meaningless stimulus**
  - **“cry wolf” effect**
  - **learn not to respond to repeated occurrences of stimulus**



Cognition and Problem Solving

- **Connects behavior with nervous system**
- **Cognition – ability of an animal's nervous system to perceive, store, process, and use information gathered by sensory receptors**

Social behaviors

- **Contests for resources**
  - **Develop as evolutionary adaptations**
  - **Agonistic behaviors**
    - **Threatening & submissive rituals**
    - **Symbolic; usually no harm done**

Social behaviors

- **Dominance hierarchy**
  - **Social ranking within a group**
    - **Pecking order**

Social behaviors

- **Territoriality**

Social behaviors

- **Altruistic behavior**
  - **Reduces individual fitness but increases fitness of recipient; selflessness**
  - **Examples:**
    - **Belding ground squirrels**
    - **Bees**
    - **Naked mole rats**

Altruism

- **Many social behaviors are selfish**
- **Natural selection favors behavior that maximizes an individual's survival and reproduction**
- ***How can altruistic behavior be explained??***
- **inclusive fitness – the total effect an individual has on proliferating its genes by producing its own offspring and by providing aid that enables close relatives to produce offspring**

Inclusive fitness

- **When parents risk (or sacrifice) their own well-being to produce & aid offspring, it increases their evolutionary fitness because it maximizes their genetic contribution to the population.**

killdeer

killdeer eggs

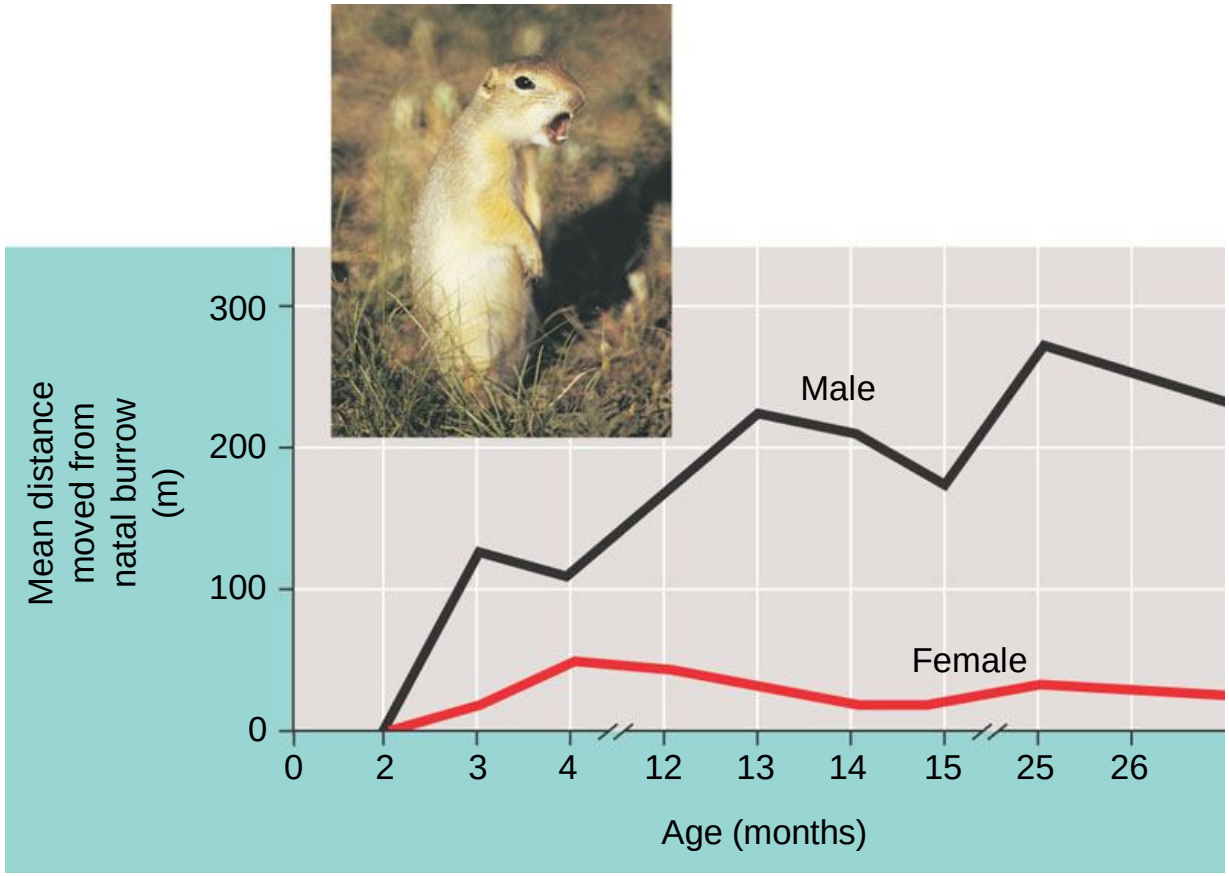
“injured” killdeer decoy behavior

Inclusive fitness

- In Belding ground squirrels, **alarm calls** to warn others of danger are usually sounded by **females**, increasing their risk of being killed
- Females are more likely to sound alarms when **close relatives** are nearby

Inclusive fitness

- **Males tend to disperse farther from birthplace than females, so females are more likely to be near close relatives**



Inclusive fitness

- **Naked mole rats live in arid regions of Africa in underground colonies of 75-250**
- **Colony = single queen, several kings, and hundreds of nonreproductive individuals (workers)**

Inclusive fitness

- **In naked mole rat populations**
  - **Nonreproductive individuals may sacrifice their lives protecting the reproductive individuals from predators**

Kin selection

- **the natural selection that favors this kind of altruistic behavior by enhancing reproductive success of relatives**

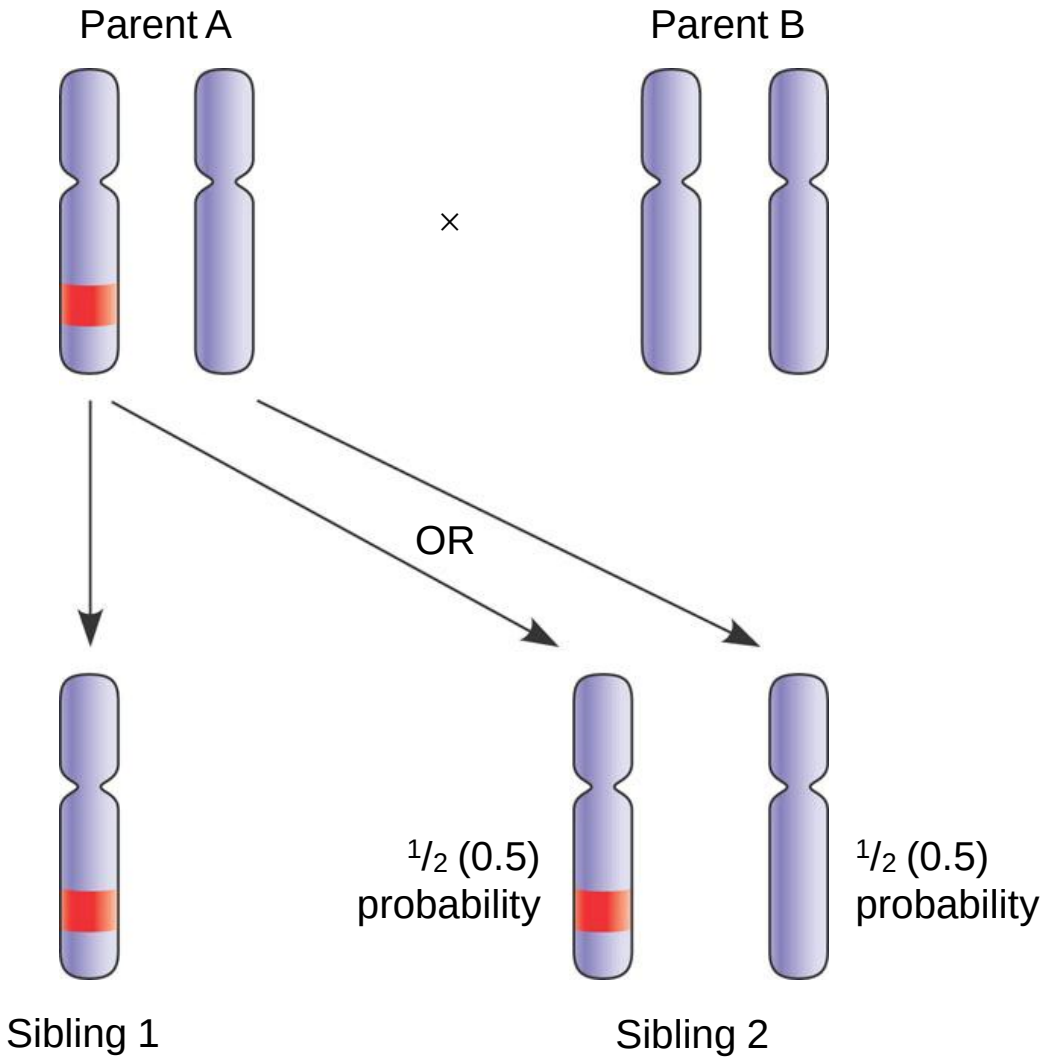
Hamilton's Rule and Kin Selection

- **Hamilton proposed a quantitative measure for predicting when natural selection would favor altruistic acts among related individuals**

- **Three variables:**
  - **benefit to recipient (B) = how many extra offspring recipient produces**
  - **cost to altruist (C) = how many fewer offspring altruist produces**
  - **coefficient of relatedness (r)**

Coefficient of relatedness

- **probability that two relatives may share the same genes**



Hamilton's Rule and Kin Selection

- **Natural selection favors altruism when the benefit to the recipient multiplied by the coefficient of relatedness exceeds the cost to the altruist:**

$$rB > C$$

- **Kin selection weakens with hereditary distance**
- **As expected, observed examples of kin selection involve close relatives (ground squirrels, bees, mole rats)**

Reciprocal Altruism

- **Altruistic behavior toward unrelated individuals**
  - **baboons may help unrelated companions in a fight**
  - **wolf may offer food to unrelated wolf**
- **Can be adaptive if the aided individual returns the favor in the future**
- **Rare in animals**
- **Limited to species with stable social groups (together long enough to return the favor)**

Reproductive Behavior

- **Reproductive behavior includes:**
  - **Seeking mates**
  - **Choosing among potential mates**
  - **Competing for mates**
  - **Caring for offspring (in some species)**

Courtship behavior

- **behavior patterns that lead up to copulation (or gamete release for external fertilization)**
- **evolutionary result of sexual selection**
- ***Why have such elaborate courtship behaviors?***

1. **Identify mates of same species**
2. **Identify physiological readiness of mate**
3. **Identify physical & genetic health of mate**

Parental investment

- **Time & resources an individual must spend to produce & nurture offspring**
  - **Eggs are generally larger & energetically more expensive to produce than sperm**
  - **For most species, males have a lower investment per offspring**
  - **<u>Reproductive success</u>:**

Quantity vs. Quality!

- **In males – higher if he fertilizes eggs of many females**
- **Females – higher if fewer offspring are more vigorous**

Mating Systems and Mate Choice

- **The mating relationship between males and females varies a great deal from species to species**
  - **Promiscuous – no strong pair-bonds or lasting relationships**
  - **Monogamous – 1 male & female mate for long time (even for life)**
  - **Polygamous – 1 individual mating with several others**
    - **Polygyny – 1 male & many females**
    - **Polyandry – 1 female & many males**

- **The needs of the young**
  - **Are an important factor constraining the evolution of mating systems**
  - **Ex. birds require care from both parents; often monogamous**
- **The certainty of paternity**
  - **Influences parental care and mating behavior**
  - **Relatively low in most species with internal fertilization (mating & birth/egg laying separated in time)**

- **In species with external fertilization, parental care is at least as likely to be carried out by males as females**

monogamy

- One male mates with one female
  - Males & females look similar

Trumpeter swans

polygyny

- **One male mates with many females**
  - **The males are often more showy and larger than the females**

polyandry

- **One female mates with many males**
  - **The females are often more showy than the males**
  - **Relatively rare**

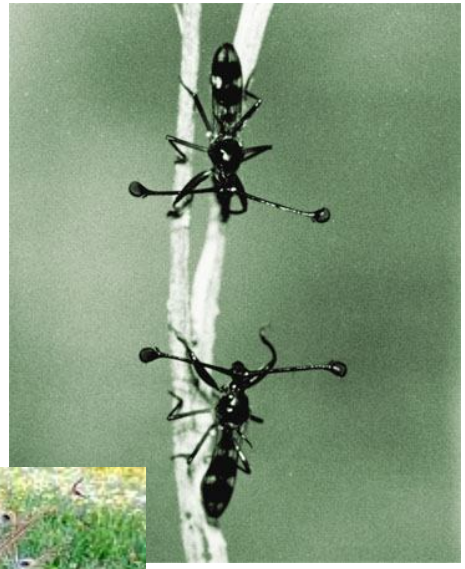
(c) In polyandrous species, such as these Wilson's phalaropes, females (top) are generally more ornamented than males.

Sexual Selection and Mate Choice

- **intersexual selection**
  - **Members of one sex choose mates on the basis of particular characteristics**
  - **Ex. mate choice by females**
- **intrasexual selection**
  - **competition among members of one sex for mates**
  - **Ex. male competition for mates**

Mate choice by females

- **Males are more ornate than females, a trait that may affect mate choice by the females**



Male Competition for Mates

- may involve agonistic behavior
- An often ritualized contest that determines which competitor gains access to a resource
  - source of intrasexual selection that can reduce variation among males

Animal Signals and Communication

- **Signal – behavior that causes a change in another animal's behavior**
- **Communication – reception of and response to signals**

Animal Signals and Communication

- **Animals communicate using**
  - **Visual, auditory, chemical (olfactory), tactile, and electrical signals**
- **Type of signal is closely related to an animal's lifestyle and environment**
  - **Most terrestrial mammals are nocturnal so more olfactory & auditory**
  - **Most birds are diurnal so more visual & auditory**

Chemical Communication

- **Many animals that communicate through odors**
  - **Emit chemical substances called pheromones**

Chemical Communication

- **injured minnow or catfish releases alarm substance that disperses in the water, inducing a fright response among fish in the area**

(a) Minnows are widely dispersed in an aquarium before an alarm substance is introduced.

(b) Within seconds of the alarm substance being introduced, minnows aggregate near the bottom of the aquarium and reduce their movement.

Are we humans locked into our genotypes?