Chapter 51

Behavioral Ecology

PowerPoint Lectures for

*Biology, Seventh Edition*

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Overview: Studying Behavior

- Humans have probably studied animal behavior for as long as we have lived on Earth
- As hunters, knowledge of animal behavior was essential to human survival
• Cranes are birds that have captivated people’s interest, possibly because they are large and their behavior is easily observed
Behavioral ecology extends observations of animal behavior by studying how such behavior is controlled and how it develops, evolves, and contributes to survival and reproductive success.
Concept 51.1: Behavioral ecologists distinguish between proximate and ultimate causes of behavior

- Scientific questions about behavior can be divided into two classes:
  - Those that focus on the immediate stimulus and mechanism for the behavior
  - Those that explore how the behavior contributes to survival and reproduction
What Is Behavior?

• Behavior is what an animal does and how it does it
• Behavior includes muscular and nonmuscular activity
• Learning is also considered a behavioral process
Proximate and Ultimate Questions

• Proximate, or “how,” questions focus on:
  – Environmental stimuli that trigger a behavior
  – Genetic, physiological, and anatomical mechanisms underlying a behavior

• Ultimate, or “why,” questions focus on evolutionary significance of a behavior
Ethology

- Ethology is the scientific study of animal behavior, particularly in natural environments
• Ethologists developed a conceptual framework defined by a set of questions

• These questions highlight the complementary nature of proximate and ultimate perspectives
Fixed Action Patterns

- A fixed action pattern (FAP) is a sequence of unlearned, innate behaviors that is unchangeable.
- Once initiated, it is usually carried to completion.
- A FAP is triggered by an external sensory stimulus known as a sign stimulus.
• In male stickleback fish, the stimulus for attack behavior is the red underside of an intruder.
• When presented with unrealistic models, as long as some red is present, the attack behavior occurs
BEHAVIOR: A male stickleback fish attacks other male sticklebacks that invade its nesting territory.

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.
Imprinting

- Imprinting is a behavior that includes learning and innate components and is generally irreversible.
- It is distinguished from other learning by a sensitive period.
- A sensitive period is a limited developmental phase that is the only time when certain behaviors can be learned.
• An example of imprinting is young geese following their mother

• Konrad Lorenz showed that when baby geese spent the first few hours of their life with him, they imprinted on him as their parent

• There are proximate and ultimate causes of this type of behavior
BEHAVIOR: Young geese follow and imprint on their mother.

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 biologists have taken advantage of imprinting in programs to save the whooping crane from extinction
Concept 51.2: Many behaviors have a strong genetic component

- Biologists study how genes and environment influence development of behavioral phenotypes.
- Innate behavior is developmentally fixed and under strong genetic influence.
Directed Movements

- Many animal movements are under substantial genetic influence
- They are called directed movements
A kinesis is a simple change in activity or turning rate in response to a stimulus.

For example, sow bugs become more active in dry areas and less active in humid areas.
(a) Kinesis increases the chance that a sow bug will encounter and stay in a moist environment.
Taxis

- A taxis is a more or less automatic, oriented movement toward or away from a stimulus.
- Many stream fish exhibit positive rheotaxis; they automatically swim in an upstream direction.
- This taxis prevents them from being swept away and keeps them facing the direction from which food will come.
(b) Positive rheotaxis keeps trout facing into the current, the direction from which most food comes.
Many features of migratory behavior in birds have been found to be genetically programmed.
Animal Signals and Communication

• In behavioral ecology, a signal is a behavior that causes a change in another animal’s behavior

• Communication is the reception of and response to signals
• Animals communicate using visual, auditory, chemical, tactile, and electrical signals

• The type of signal is closely related to lifestyle and environment
Chemical Communication

• Many animals that communicate through odors emit chemical substances called pheromones.

• When a minnow or catfish is injured, an alarm substance in the fish’s skin 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.
Auditory Communication

- Experiments with insects have shown that courtship songs are under genetic control
SONOGRAMS

Chrysoperla plorabunda parent

Volley period

Standard repeating unit

Vibration volleys

crossed with

Chrysoperla johnsoni parent

Volley period

Standard repeating unit

F₁ hybrids, typical phenotype

Volley period

Standard repeating unit
Genetic Influences on Mating and Parental Behavior

- A variety of mammalian behaviors are under relatively strong genetic control
- Research has revealed the genetic and neural basis for mating and parental behavior of male prairie voles
Concept 51.3: Environment, interacting with an animal’s genetic makeup, influences the development of behaviors

- Research has revealed that environmental conditions modify many of the same behaviors.
Dietary Influence on Mate Choice Behavior

- An example of environmental influence is the role of diet in mate selection by *Drosophila mojavensis*.
- Experiments have demonstrated that food eaten by larvae influences later mate choice in females.
With Sonoran males
With Baja males

Proportion of matings by Sonoran females

(a)

(b)

Culture medium

Artificial

Organ pipe cactus

Agria cactus
• Therese Markow and Eric Toolson proposed that the physiological basis for the observed mate preferences was differences in hydrocarbons in the exoskeletons of the flies
Social Environment and Aggressive Behavior

- Studies of California mice and white-footed mice have uncovered an influence of social environment on aggressive and parental behaviors
<table>
<thead>
<tr>
<th>Species</th>
<th>Aggression Toward an Intruder</th>
<th>Aggression in Neutral Situation</th>
<th>Paternal Behavior</th>
<th>Arginine-Vasopressin (AVP) Content in Brain</th>
</tr>
</thead>
<tbody>
<tr>
<td>California mice fostered by white-footed mice</td>
<td>Reduced</td>
<td>No difference</td>
<td>Reduced</td>
<td>Reduced</td>
</tr>
<tr>
<td>White-footed mice fostered by California mice</td>
<td>No difference</td>
<td>Increased</td>
<td>No difference</td>
<td>No difference</td>
</tr>
</tbody>
</table>

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

Learning

• Learning is modification of behavior based on specific experiences

• Learned behaviors range from very simple to very complex
Habituation

- Habituation is a simple form of learning that involves loss of responsiveness to stimuli that convey little or no information.

- For example, a hydra contracts when disturbed by a slight touch, but it stops responding if repeatedly disturbed without further consequences.
Spatial Learning

- Spatial learning is a more complex modification of behavior based on experience with the spatial structure of the environment.
- Niko Tinbergen showed how digger wasps use landmarks to find nest entrances.
Cognitive Maps

- A cognitive map is an internal representation of spatial relationships between objects in an animal’s surroundings.
Associative Learning

• In associative learning, animals associate one feature of their environment with another.

• Classical conditioning is a type of associative learning in which an arbitrary stimulus is associated with a reward or punishment.
Before stimulus
Influx of water alone
Influx of alarm substance
Influx of pike odor

Relative activity level

Day 1
Control group
Experimental group
Day 3
Control group
Experimental group

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Operant conditioning is a type of associative learning in which an animal learns to associate one of its behaviors with a reward or punishment. It is also called trial-and-error learning.
Cognition and Problem Solving

- Cognition is the ability of an animal’s nervous system to perceive, store, process, and use information gathered by sensory receptors.

- Problem solving can be learned by observing behavior of other animals.
Genetic and Environmental Interaction in Learning

- Genetics and environment can interact to influence the learning process
Concept 51.4: Behavioral traits can evolve by natural selection

- Because genes influence behavior, natural selection can result in evolution of behavioral traits in populations
Behavioral Variation in Natural Populations

• When behavioral variation within a species corresponds to environmental variation, it may be evidence of past evolution
Variation in Prey Selection

- Differences in prey selection in populations of garter snakes are due to prey availability and are evidence of behavioral evolution
(a) A garter snake
(*Thamnophis elegans*)

(b) A banana slug (*Ariolimus californicus*); not to scale
Variation in Aggressive Behavior

• Funnel spiders living in different habitats exhibit differing degrees of aggressiveness in defense and foraging behavior
Experimental Evidence for Behavioral Evolution

- Laboratory and field experiments can demonstrate the evolution of behavior
Laboratory Studies of Drosophila Foraging Behavior

- Studies of *Drosophila* populations raised in high- and low-density conditions show a clear divergence in behavior linked to specific genes
**Low population density**

**High population density**

**Average path length (cm)**

- **L1**: 8 cm
- **L2**: 8 cm
- **L3**: 7 cm
- **H1**: 14 cm
- **H2**: 14 cm
- **H3**: 12 cm
- **H4**: 12 cm
- **H5**: 10 cm

*D. melanogaster* lineages
Migratory Patterns in Blackcaps

- Field and laboratory studies of blackcap birds provided evidence of a genetic basis for migratory orientation.

- Birds placed in funnel cages left marks indicating the direction they were trying to migrate.
(a) Blackcaps placed in a funnel cage left marks indicating the direction in which they were trying to migrate.
• Migratory orientation of wintering adult birds captured in Britain was very similar to that of their laboratory-raised offspring.

• Offspring of British blackcaps and young birds from Germany were raised under similar conditions but showed very different migratory orientations.
Wintering blackcaps captured in Britain and their laboratory-raised offspring had a migratory orientation toward the west, while young birds from Germany were oriented toward the southwest.

(b) Wintering blackcaps captured in Britain and their laboratory-raised offspring had a migratory orientation toward the west, while young birds from Germany were oriented toward the southwest.
Concept 51.5: Natural selection favors behaviors that increase survival and reproductive success

• Genetic components of behavior evolve through natural selection

• Behavior can affect fitness by influencing foraging and mate choice
Foraging Behavior

- Optimal foraging theory views foraging behavior as a compromise between benefits of nutrition and costs of obtaining food
Energy Costs and Benefits

- Reto Zach conducted a cost-benefit analysis of feeding behavior in crows.
- The crows eat molluscs called whelks but must drop them from the air to crack the shells.
- Optimal flight height correlated with fewer drops, indicating a trade-off between energy gained (food) and energy expended.
The graph illustrates the average number of drops and total flight height for different drop heights. The drop height preferred by crows is 5.23 m. The graph shows that as the height of the drop increases, the total flight height increases, with a peak at 5 m for the average number of drops.
• In bluegill sunfish, prey selection behavior is related to prey density
### Low prey density

<table>
<thead>
<tr>
<th>Prey Size</th>
<th>Percentage</th>
</tr>
</thead>
<tbody>
<tr>
<td>Small</td>
<td>33%</td>
</tr>
<tr>
<td>Medium</td>
<td>33%</td>
</tr>
<tr>
<td>Large</td>
<td>33%</td>
</tr>
</tbody>
</table>

### High prey density

<table>
<thead>
<tr>
<th>Prey Size</th>
<th>Percentage</th>
</tr>
</thead>
<tbody>
<tr>
<td>Small</td>
<td>14%</td>
</tr>
<tr>
<td>Medium</td>
<td>35%</td>
</tr>
<tr>
<td>Large</td>
<td>50%</td>
</tr>
</tbody>
</table>

### Percentage of prey available

- **Small prey** at far distance: 100%
- **Small prey** at middle distance: 35%
- **Small prey** at close distance: 2%

### Predicted percentage of prey in diet

- **Small prey** at far distance: 32.5%
- **Small prey** at middle distance: 32.5%
- **Small prey** at close distance: 35%

### Observed percentage of prey in diet

- **Small prey** at far distance: 2%
- **Small prey** at middle distance: 40%
- **Small prey** at close distance: 57%
Risk of Predation

- Research on mule deer populations has shown that predation risk affects where deer feed.
Relative deer use and predation risk across different habitats:

- **Open** habitat shows a higher relative deer use (approximately 60%) but lower predation risk (approximately 5%)
- **Forest edge** habitat shows a moderate relative deer use (approximately 40%) and high predation risk (approximately 15%)
- **Forest interior** habitat shows a lower relative deer use (approximately 20%) but significant predation risk (approximately 10%)

The graph indicates that deer use varies with habitat type, with forest interior being the least preferred due to high predation risk, and open areas being the most preferred due to low predation risk.
Mating Behavior and Mate Choice

- Mating behavior is the product of a form of natural selection called sexual selection.
Mating Systems and Mate Choice

• The mating relationship between males and females varies greatly from species to species

• In many species, mating is promiscuous, with no strong pair-bonds or lasting relationships
In monogamous relationships, one male mates with one female
(a) Since monogamous species, such as these trumpeter swans, are often monomorphic, males and females are difficult to distinguish using external characteristics only.
• In polygyny, one male mates with many females
• The males are often more showy and larger than the females
(b) Among polygynous species, such as elk, the male (left) is often highly ornamented.
• In polyandrous systems, one female mates with many males

• The females are often more showy than the males
(c) In polyandrous species, such as these Wilson’s phalaropes, females (top) are generally more ornamented than males.
• Needs of the young are an important factor constraining evolution of mating systems

• Certainty of paternity influences parental care and mating behavior

• 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
Eggs
Sexual Selection and Mate Choice

• In intersexual selection, members of one sex choose mates on the basis of certain traits.

• Intrasexual selection involves competition between members of one sex for mates.
Mate Choice by Females

• Male zebra finches are more ornate than females, a trait that may affect mate choice by the females.
• Imprinting of female chicks on males with more ornamentation affects mate selection as adults.
• Experiments suggest that mate choice by female zebra finches has played a key role in evolution of ornamentation in male zebra finches.
Females reared by ornamented parents or ornamented fathers preferred ornamented males as mates.

Females reared by ornamented mothers or nonornamented parents showed no preference for either ornamented or nonornamented males.

Males reared by all experimental groups showed no preference for either ornamented or nonornamented female mates.
• The size of eyestalks in stalk-eyed flies affects which males the females choose to mate with

• Studies of such behavior support the hypothesis that females base mate choices on characteristics that correlate with male quality
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.
• Morphology affects the mating behavior in isopods of the same species that are genetically distinct
Applying Game Theory

• Game theory evaluates alternative strategies where the outcome depends on each individual’s strategy and the strategy of other individuals

• Mating success of male side-blotched lizards is influenced by male polymorphism and the abundance of different males in a given area
Concept 51.6: The concept of inclusive fitness can account for most altruistic social behavior

- Many social behaviors are selfish
- Natural selection favors behavior that maximizes an individual’s survival and reproduction
Altruism

- 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.

- In naked mole rat populations, nonreproductive individuals may sacrifice their lives protecting the reproductive individuals from predators.
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
Hamilton’s Rule and Kin Selection

• 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
  – Cost to the altruist
  – Coefficient of relatedness (the probability that if two individuals share a parent or ancestor, a gene in one individual will also be present in the second individual)
Parent A \times Parent B

Sibling 1 \left( \frac{1}{2} \text{ (0.5) probability} \right)

Sibling 2 \left( \frac{1}{2} \text{ (0.5) probability} \right)
Natural selection favors altruism when the benefit to the recipient multiplied by the coefficient of relatedness exceeds the cost to the altruist.

This inequality is called Hamilton’s rule.

Kin selection is the natural selection that favors this kind of altruistic behavior by enhancing reproductive success of relatives.

An example of kin selection and altruism is the warning behavior in Belding’s ground squirrels.
Mean distance moved from natal burrow (m) vs. Age (months)

- **Male**: Generally increases with age, peaking around 12 months.
- **Female**: Remains relatively constant with a slight increase at the end of the timeline.

- **300 m**
- **200 m**
- **100 m**
- **0 m**
Reciprocal Altruism

- Altruistic behavior toward unrelated individuals can be adaptive if the aided individual returns the favor in the future
- This type of altruism is called reciprocal altruism
Social Learning

- Social learning forms the roots of culture
- Culture is a system of information transfer through observation or teaching that influences behavior of individuals in a population
Mate Choice Copying

- In mate choice copying, individuals in a population copy the mate choice of others.
- This type of behavior has been extensively studied in the guppy *Poecilia reticulata*. 
Female guppies prefer males with more orange coloration.

Male guppies with varying degrees of coloration

Control Sample

Female model engaged in courtship with less orange male

Female guppies prefer less orange males that are associated with another female.

Experimental Sample
Social Learning of Alarm Calls

• Vervet monkeys produce a complex set of alarm calls
• Infant monkeys give undiscriminating calls but learn to fine-tune them by the time they are adults
No other species comes close to matching the social learning and cultural transmission that occurs among humans.
Evolution and Human Culture

• Human culture is related to evolutionary theory in the distinct discipline of sociobiology

• Human behavior, like that of other species, results from interactions between genes and environment

• However, our social and cultural institutions may provide the only feature in which there is no continuum between humans and other animals