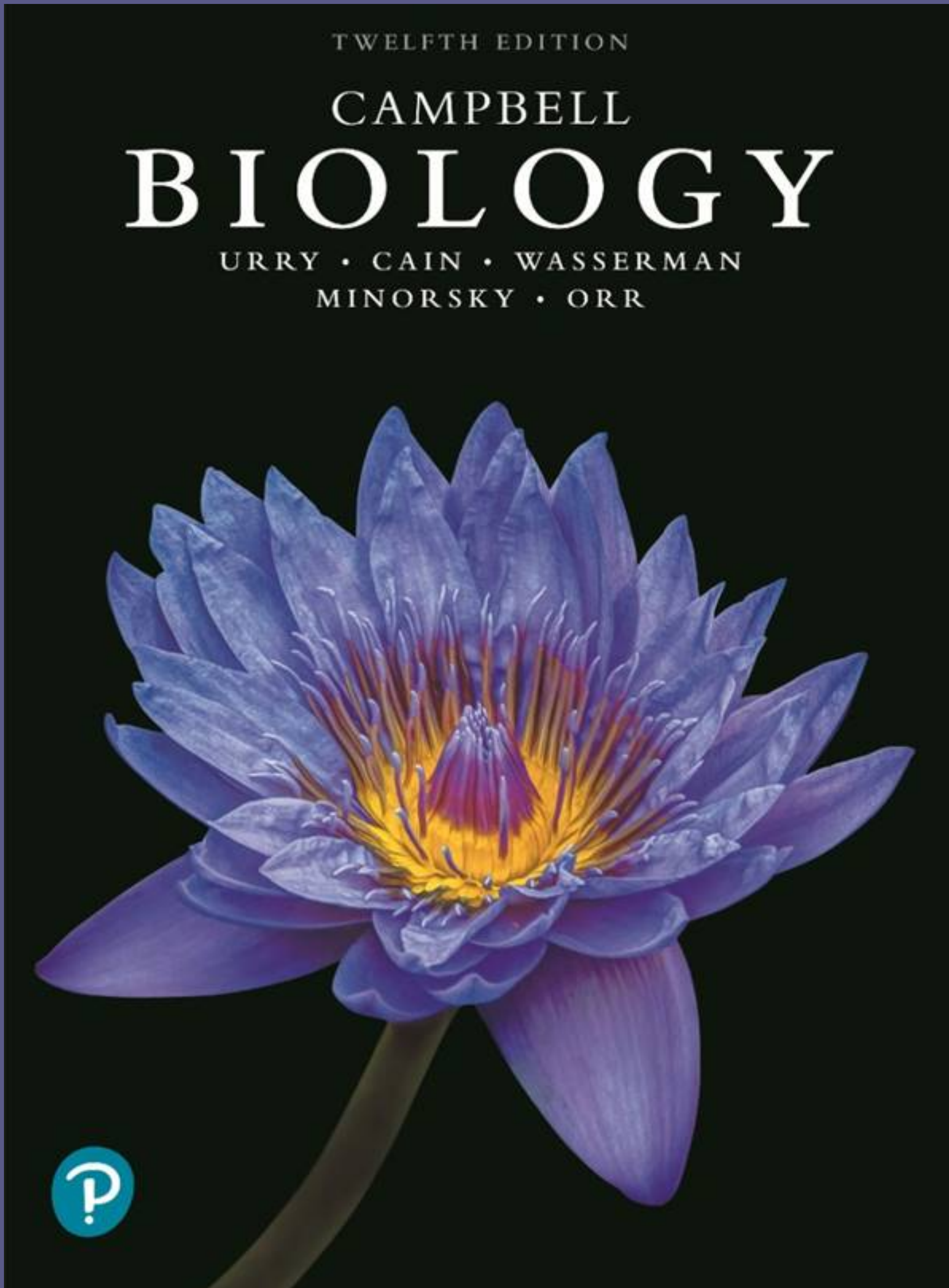


Chapter 51

Animal Behavior

Lecture Presentations by
Nicole Tunbridge and
Kathleen Fitzpatrick

Figure 51.1a

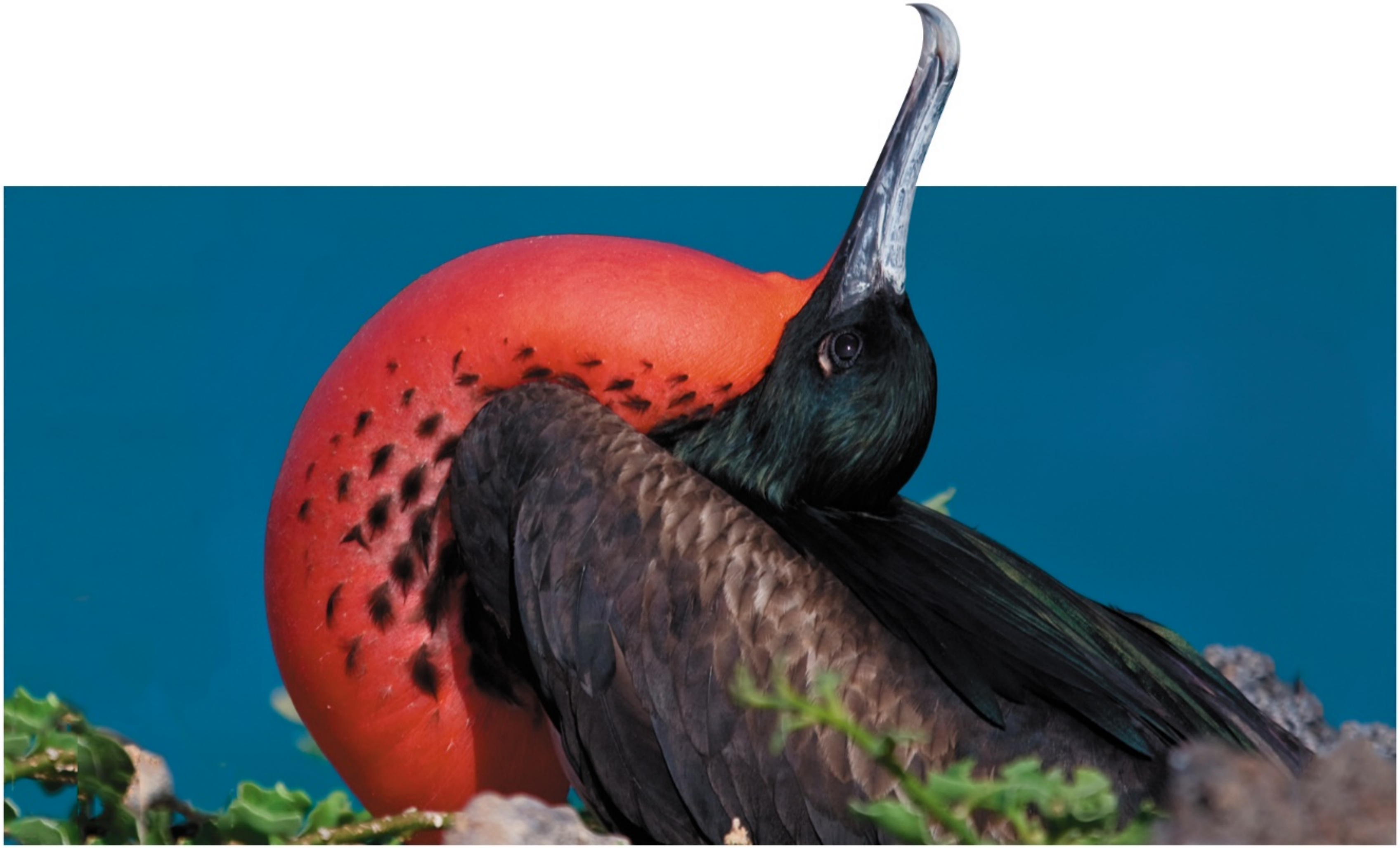
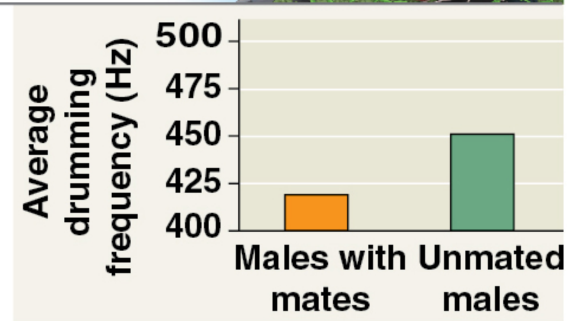


Figure 51.1b

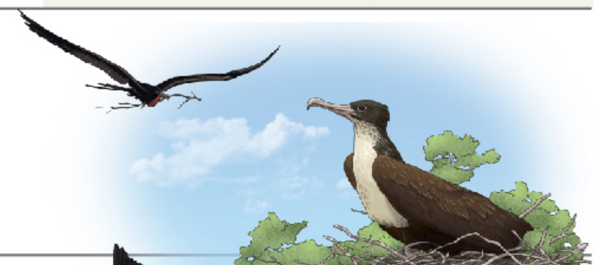
What questions do biologists seek to answer in studying animal behavior?

1. What event or signal triggers the behavior?

2. How does experience during growth and development influence the behavior?



3. How does the behavior aid survival and reproduction?



4. How has the behavior been shaped by natural selection?

Answering these questions can provide fundamental insights into how behaviors occur and why they arise.

CONCEPT 51.1: Discrete sensory inputs can stimulate both simple and complex behaviors

- A **behavior** is an action carried out by muscles under control of the nervous system
  - For example, when an animal uses its throat muscles to produce a song
- Behaviors and the anatomical structures related to their performance are subject to natural selection

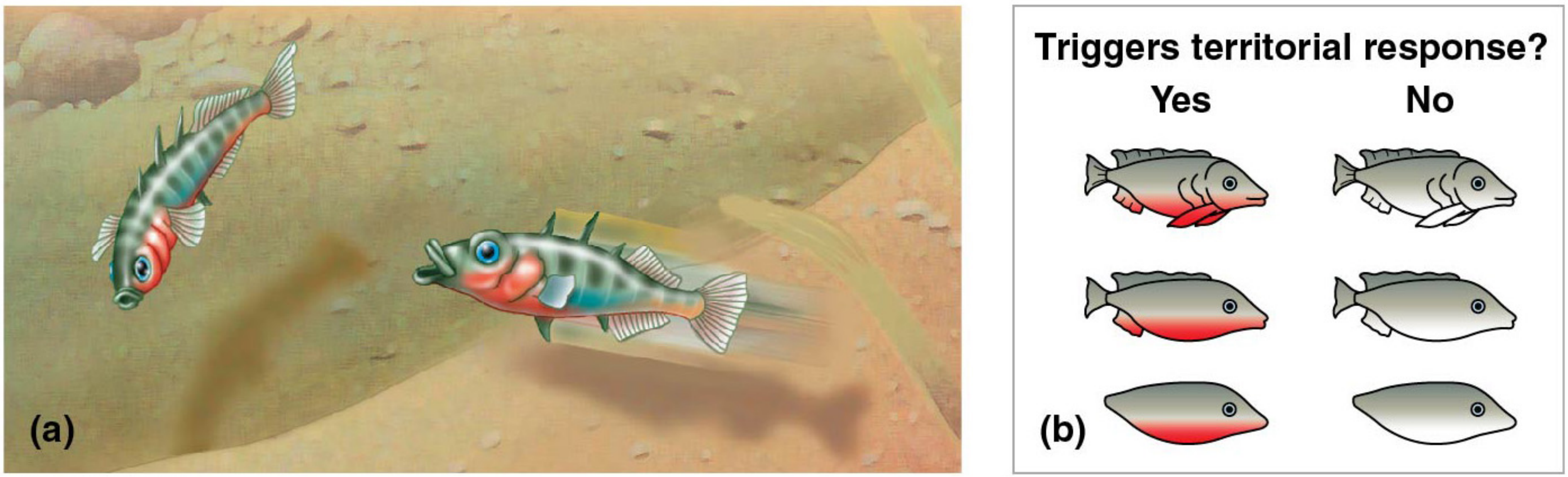
- Niko Tinbergen identified four questions that should be answered to understand animal behavior
  1. What stimulus elicits the behavior, and how do the various body systems bring it about?
  2. How does the animal's experience during growth and development influence the response?
  3. How does the behavior aid survival and reproduction?
  4. What is the behavior's evolutionary history?

- The first two questions ask about proximate causation—*how* a behavior occurs or is modified
- The last two ask about ultimate causation—*why* a behavior occurs in the context of natural selection
- Ultimate causation is central to **behavioral ecology**, the study of the ecological and evolutionary basis for animal behavior

Fixed Action Patterns

- Niko Tinbergen observed male stickleback fish in the lab responding aggressively to a passing red truck
- In sticklebacks, the proximate cause of male attack behavior is the red underside of a male intruder
- Males do not attack fish lacking red coloration, but will attack even unrealistic models with red color

Figure 51.2



- A **fixed action pattern** is a sequence of unlearned acts directly linked to an external cue called a **sign stimulus**
  - For example, the attacking behavior in sticklebacks is a fixed action pattern that happens in response to a red object, the sign stimulus
- Fixed action pattern behaviors are unchangeable and, once initiated, usually carried to completion

Migration

- **Migration** is a regular, long-distance change in location guided by environmental cues
- Animals can orient themselves through unfamiliar territory using their position relative to
  - The sun
  - The North Star
  - Earth’s magnetic field

Behavioral Rhythms

- Some animal behaviors are affected by the circadian rhythm, a daily cycle of rest and activity
- The circadian rhythm is regulated by the circadian clock, an internal mechanism with 24-hour periodicity
- The clock is usually synchronized with light and dark cycles, but can maintain rhythm even in constant conditions

- Behaviors such as migration and reproduction are linked to changing seasons, or a circannual rhythm
- These behaviors correlate with food availability, but are not a direct response to food intake
- Periods of daylight and darkness in the environment are common seasonal cues

- Some biological rhythms are linked to lunar cycles, which affect tide movements
  - For example, male fiddler crabs perform courtship displays during the new or full moon, when tidal movements are at their greatest
  - Larvae are dispersed to deeper waters—where they complete early development—by the heavy tides

Figure 51.3

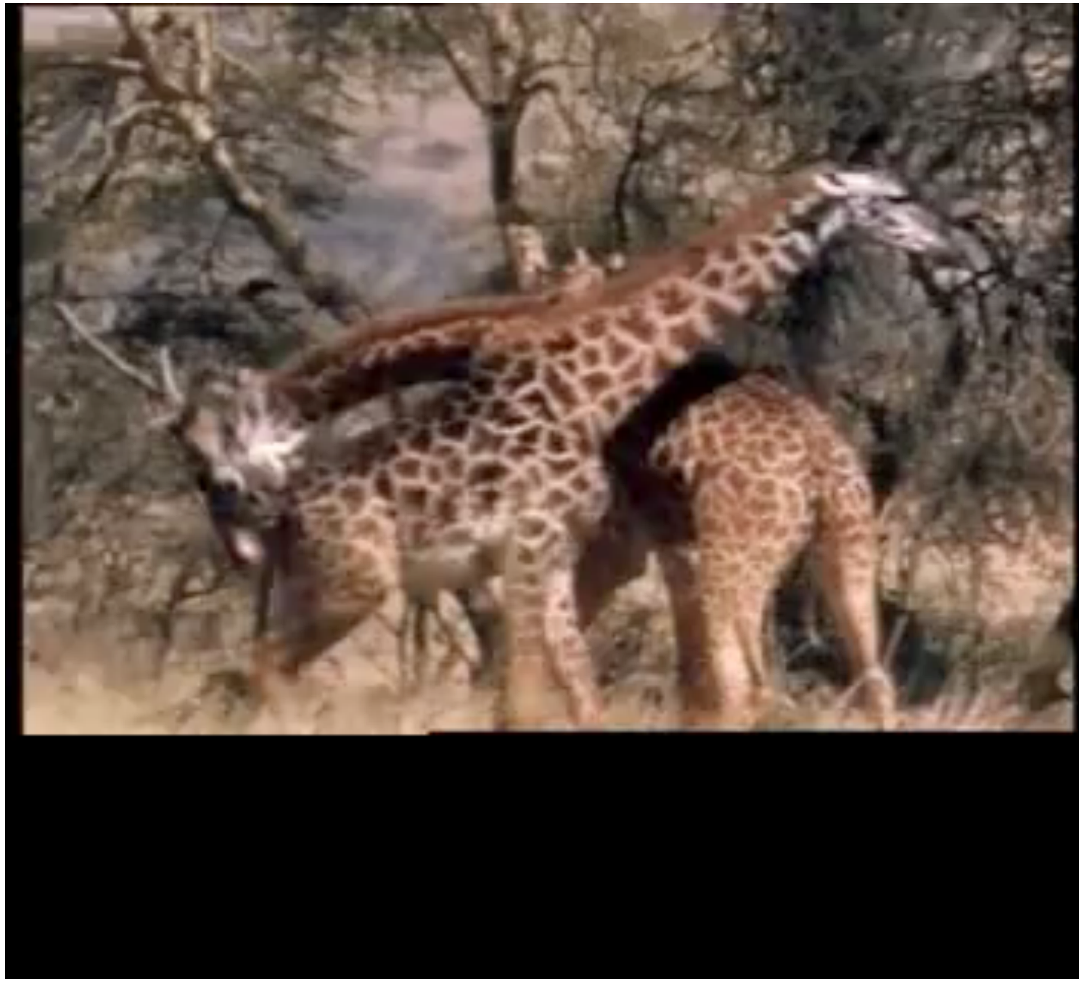
Animal Signals and Communication

- A **signal** is a stimulus generated by one animal that guides the behavior of another
  - For example, when male fiddler crabs wave their large claw, it is a signal for females to select them as mates
- **Communication** is the transmission and reception of signals between animals

Video: Albatross Courtship Ritual

Video: Blue-footed Boobies Courtship Ritual

Video: Giraffe Courtship Ritual



Forms of Animal Communication

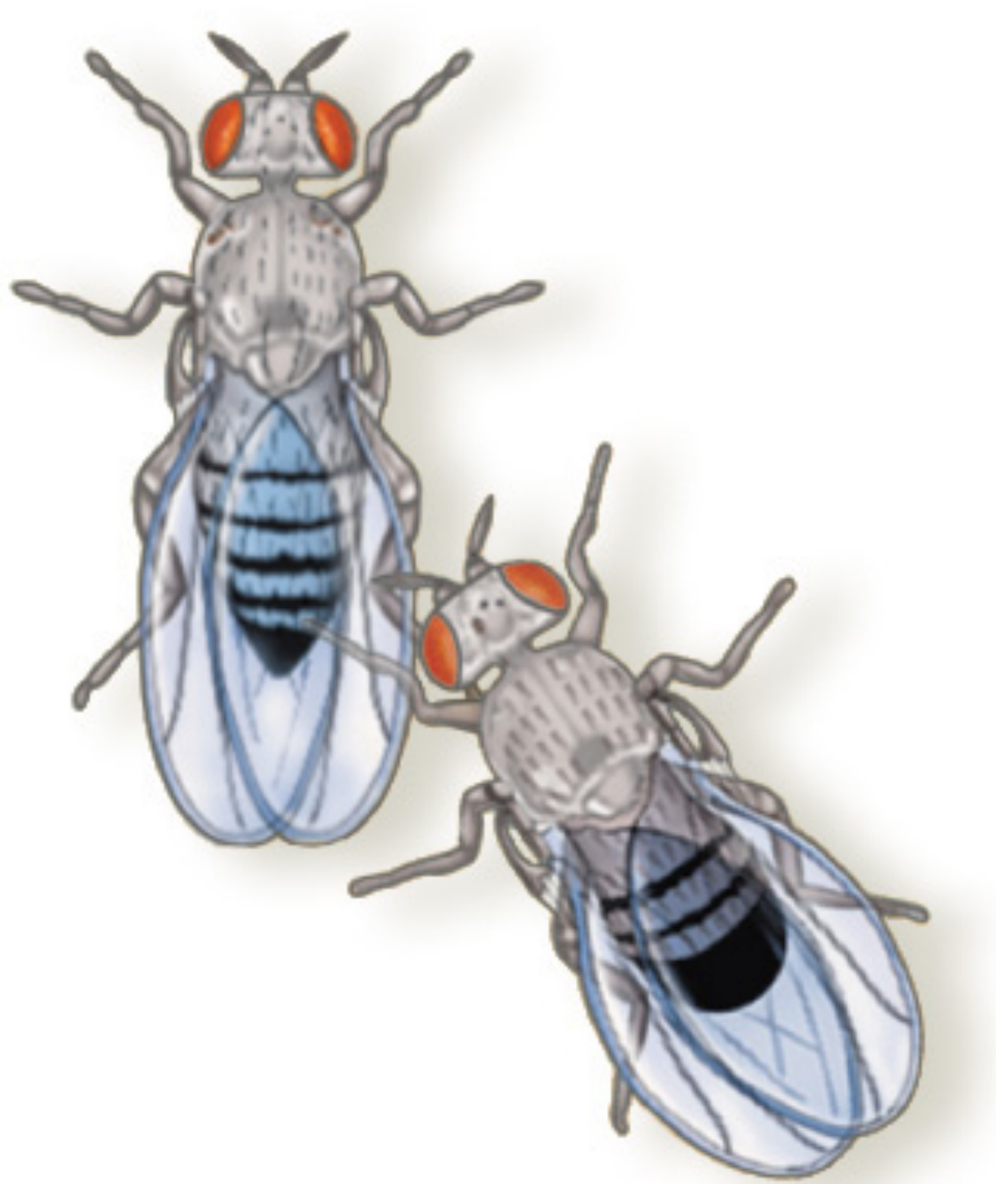
- There are four common modes of communication in animals: visual, chemical, tactile, and auditory
- In a stimulus-response chain, the response to each stimulus is itself a stimulus for the next behavior

- Fruit fly courtship involves a three-step stimulus-response chain using all four communication types
- If all three steps are successful, the female will allow the male to copulate

1. A male identifies a female of the same species
   - Visual communication: He sees the female and orients his body toward hers
   - Chemical communication: He smells chemicals the female releases into the air to confirm her identify

2. The male alerts the female to his presence
   – Tactile communication: He touches the female with a foreleg
3. The male produces a courtship song to inform the female of his species
   – Auditory communication: He extends and vibrates his wing

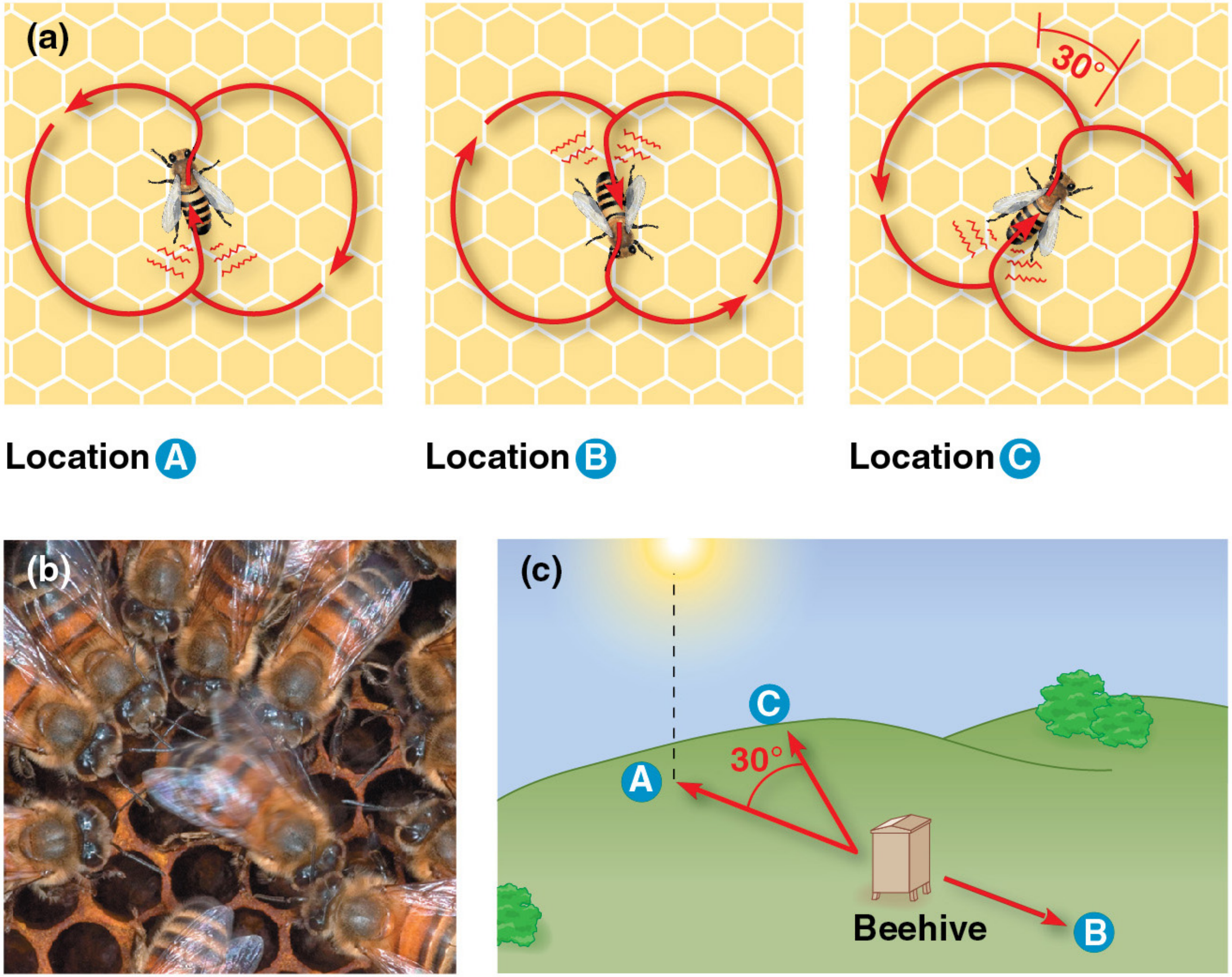
Figure 51.4



- The information content of communication is variable
- Honeybees show complex communication with symbolic language
- A bee returning from the field performs a “waggle dance” to communicate information about the distance and direction of a food source

- The angle of the straight-run relative to the vertical surface of the hive indicates the direction to the food
- The number of abdominal waggles in the straight-run indicates the distance to the food
- If food is less than 50 m away, the bee moves in tight circles while moving its abdomen side to side

Figure 51.5



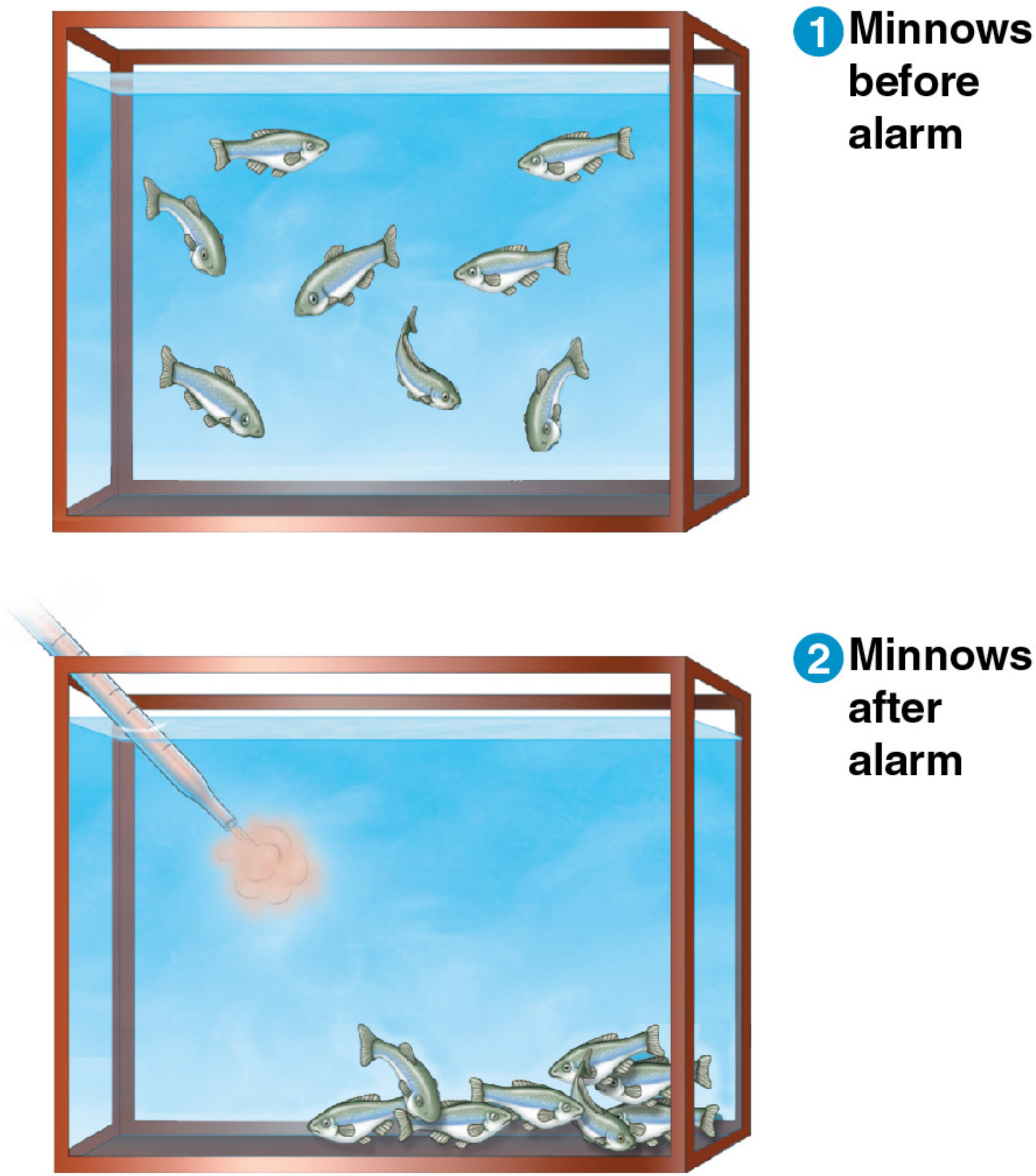
Video: Bee Pollinating

Pheromones

- Animals that communicate through odors or tastes emit chemical substances called **pheromones**
  - For example, when a minnow is injured, an alarm substance is released from its skin, inducing a fright response among other minnows in the area

- Pheromones can be very effective at remarkably low concentrations
  - For example, just 1 cm^2 of skin from a fathead minnow contains enough alarm substance to induce a reaction in 58,000 L of water

Figure 51.6



CONCEPT 51.2: Learning establishes specific links between experience and behavior

- **Innate behavior**—such as a fixed action pattern or pheromone signaling—is unlearned behavior performed by all individuals the same way each time
  - For example, web building is an innate behavior in spiders
- Other behaviors are not developmentally fixed, and may vary considerably with experience

Figure 51. UN01

Experience and Behavior

- A **cross-fostering study** places the young from one species in the care of adults from another species in a similar environment
- Behavior changes in the offspring provide a measure of the influence of the environment on behavior

- Cross-fostering experiments with California mice and white-footed mice reveal an influence of the social environment on aggression and paternal behaviors
- Cross-fostered mice developed some behaviors that were consistent with those of their foster parents

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	Reduced
White-footed mice fostered by California mice	No difference	Increased	No difference

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

- **Twin studies**, comparing behavior between identical twins raised apart, are used to study the genetic and environmental basis of human behavior

Figure 51. UN02

Learning

- The capacity for learning depends on the genetically coded development of the nervous system
- **Learning** itself is the modification of behavior based on specific experiences
- Research must consider the contributions of both nature and nurture in shaping learning and behavior

Imprinting

- **Imprinting** is the establishment of a long-lasting behavioral response to a particular individual or object
- Imprinting can only take place during a specific time in development called the **sensitive period**
  – For example, among gulls, parents must bond with their offspring and the offspring must imprint on them within one to two days or the offspring will be rejected

- Many species of waterfowl have no innate recognition of “mother”; they identify with the first object they encounter that has key characteristics
  - For example, the imprint stimulus in greylag geese is any nearby object that is moving away from them
  - If their first exposure is to a human, they will imprint on the human and not recognize their biological mother

Figure 51. 7

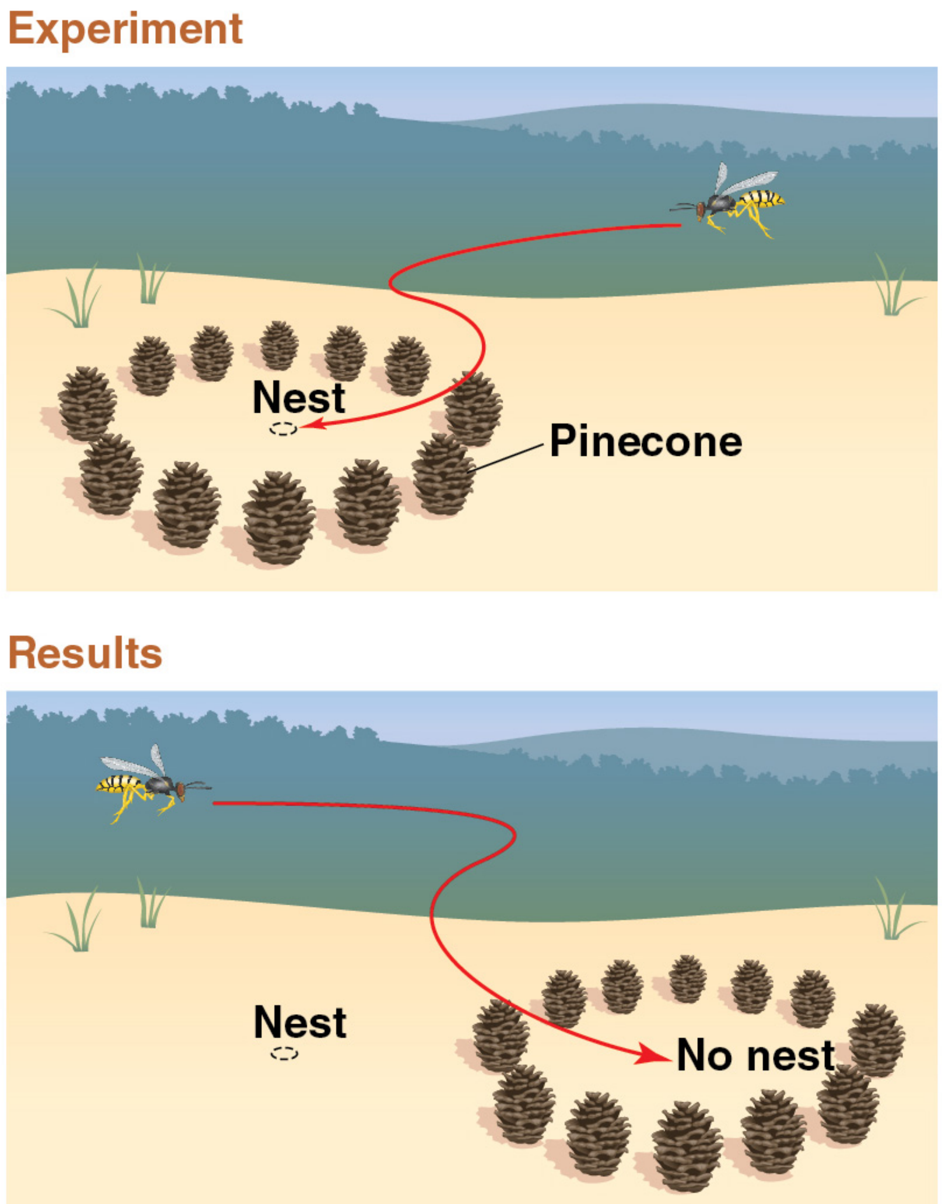
Video: Ducklings

- Conservation biologists have taken advantage of imprinting in programs to save endangered species
  - For example, whooping cranes imprint on humans wearing “crane suits” who will lead their migration in ultralight aircraft
  - Since 2016, conservation efforts have shifted focus to aim at fostering self-sustaining crane populations

Spatial Learning and Cognitive Maps

- **Spatial learning** is the establishment of a memory that reflects the environment’s spatial structure
- Niko Tinbergen showed how digger wasps use landmarks to find nest entrances

Figure 51. 8



Animation: Digger Wasps and Landmarks

Homing Behavior in Digger Wasps

The Digger Wasp

Dr. Niko Tinbergen

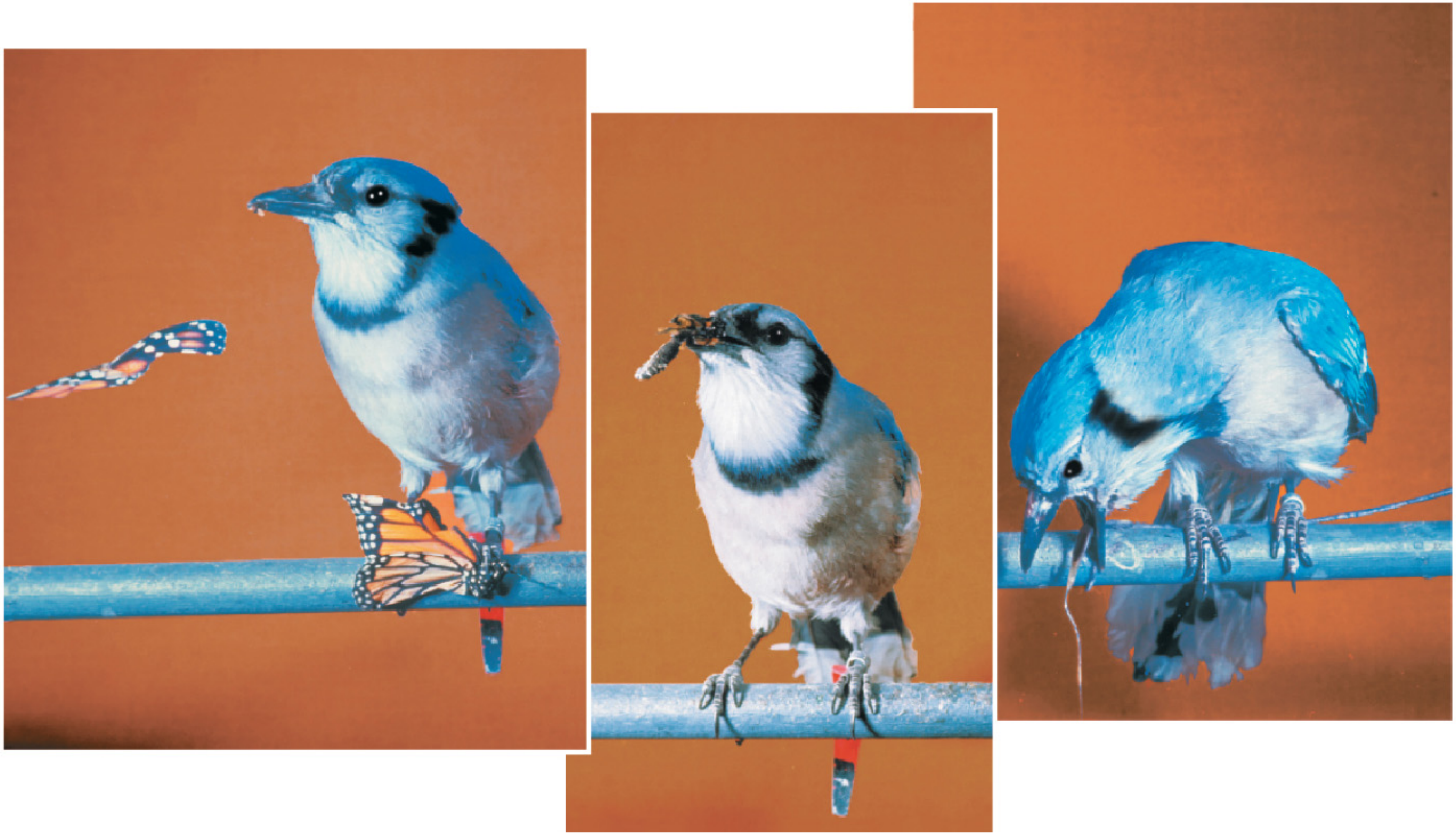
[redacted]

- Some animals learn by forming a **cognitive map**, an internal representation of the spatial relationships between objects in its surroundings
  - For example, Clark’s nutcrackers can find food hidden in caches located halfway between particular landmarks

Associative Learning

- In **associative learning**, animals associate one feature of their environment (such as color) with another (such as a foul taste)
  - For example, after an experience with a distasteful monarch butterfly, a blue jay will avoid eating all monarchs and similar-looking butterflies

Figure 51. 9



- Classical conditioning is a type of associative learning in which an arbitrary stimulus is associated with a reward or punishment
  - For example, a dog that repeatedly hears a bell before being fed will salivate in response to the sound of a bell in anticipation of a meal

- 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
  - For example, a rat that is fed after pushing a lever will learn to push the lever in order to receive food

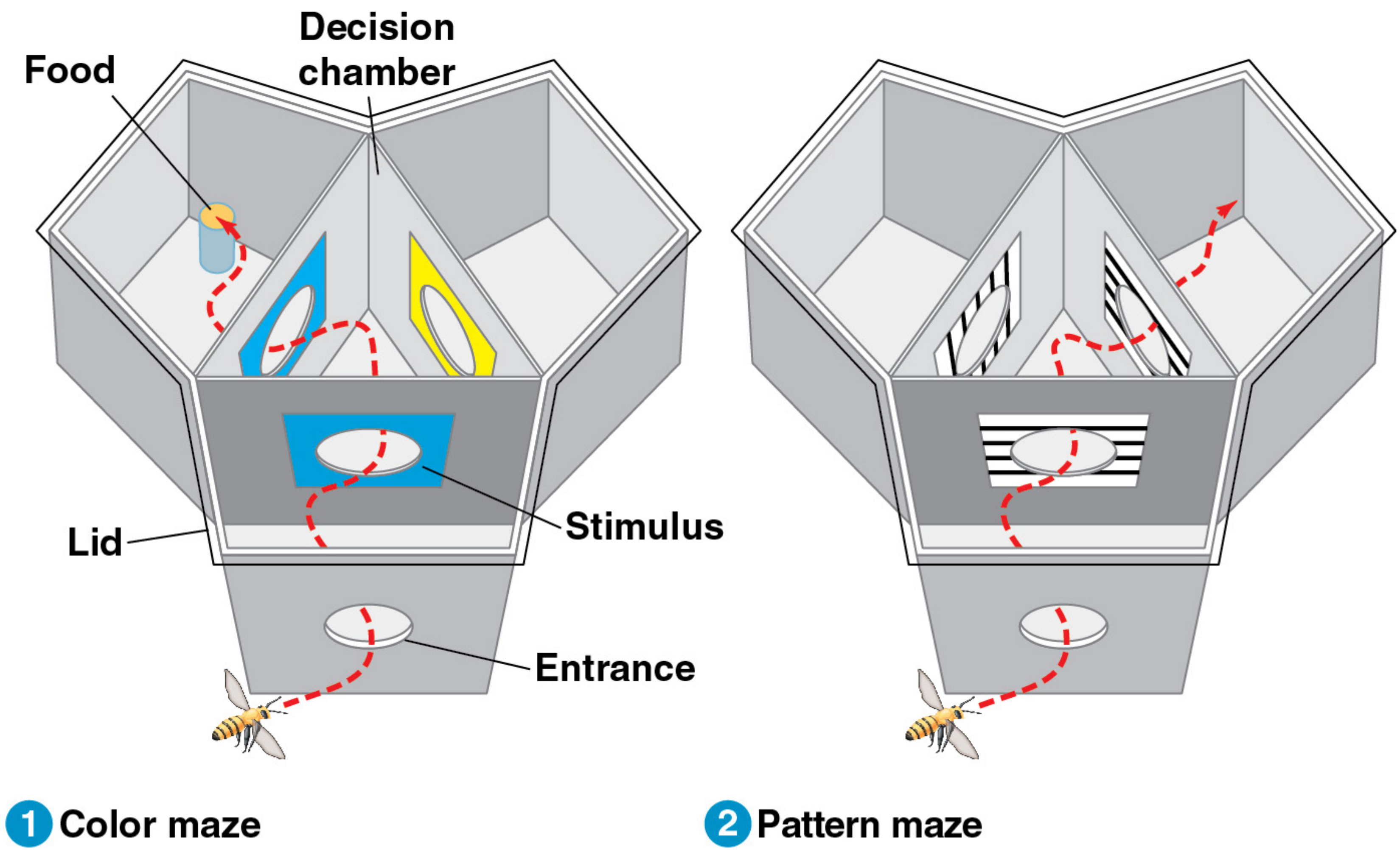
- There are limits to the pairs of environmental features that animals can learn to link
  - For example, rats can learn to avoid illness-inducing foods on the basis of smells, but not sights or sounds
- The associations an animal can make usually reflect relationships likely to occur in their environment

Cognition and Problem Solving

- The most complex forms of learning involve cognition
- **Cognition** is a process of knowing that involves awareness, reasoning, recollection, and judgment

- Initially, only primates and some marine mammals were thought to exhibit cognition
- Many other groups, including insects, now appear to exhibit cognition in controlled lab studies
  - For example, honeybees can distinguish “same” from “different” and distinguish between human faces

Figure 51.10



Decision chamber
Food
Lid
Stimulus
Entrance
1 Color maze
2 Pattern maze

- **Problem solving** is a cognitive activity of devising a strategy to overcome an obstacle
- Problem solving is highly developed in some mammals
  - For example, chimpanzees will stack boxes in order to reach suspended food

- Some bird species, particularly corvids, demonstrate complex problem solving
  - For example, ravens learn to obtain food suspended by a string by pulling up the string
  - Learning ability varied among individuals; some ravens failed to solve the problem

Development of Learned Behaviors

- Development of some behaviors occurs gradually, or in distinct stages over time
  - For example, a white-crowned sparrow memorizes the song of its species during an early sensitive period
  - In a second learning phase, the juvenile bird sings tentative notes called a subsong
  - When the song matches the one that it memorized, it “crystallizes” and the bird will sing no other adult song

Social Learning

- **Social learning** is learning by observing and interpreting behaviors and their consequences
  – For example, young chimpanzees learn to crack palm nuts with stones by copying experienced chimpanzees
  – Young vervet monkeys learn from elders how to make and respond to alarm calls distinct to specific predators

Figure 51.11

Video: Chimp Cracking Nut

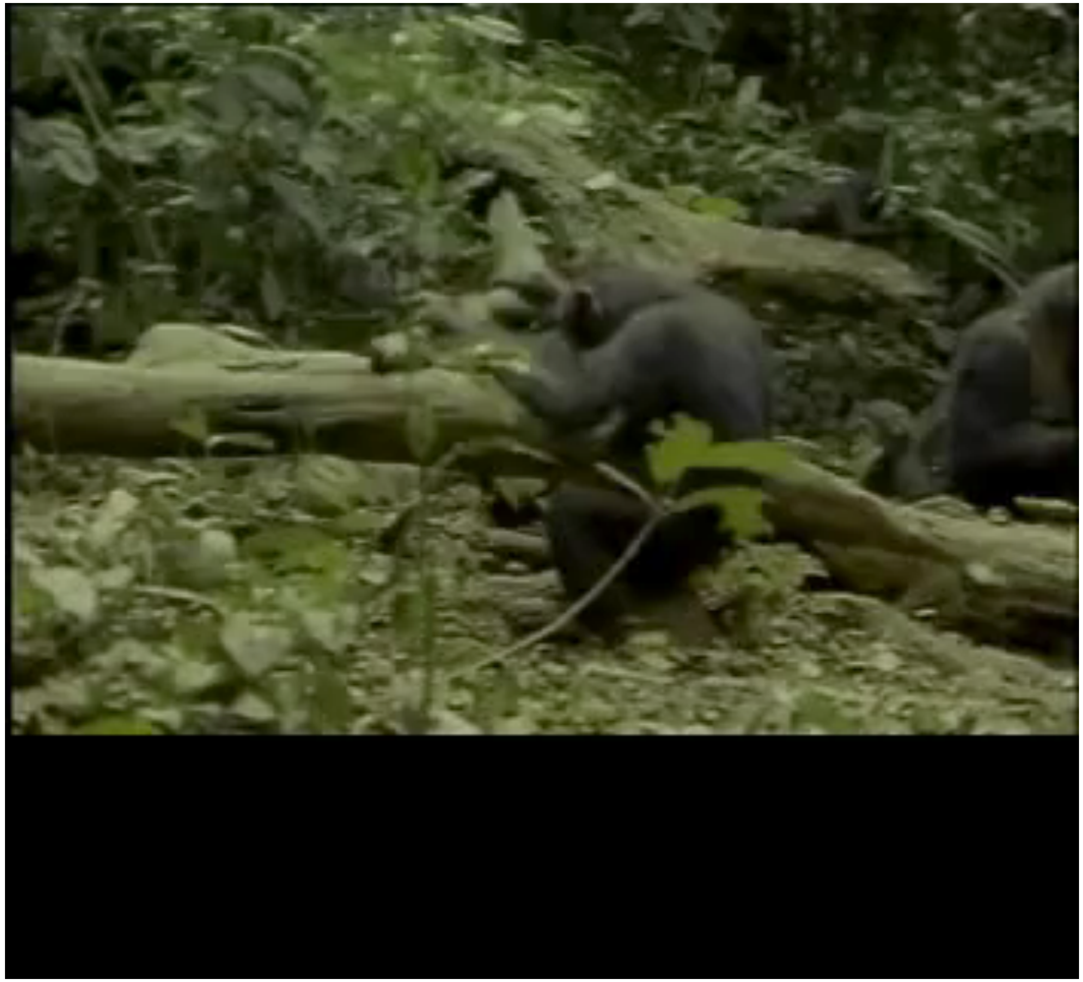


Figure 51.12

- **Culture** is a system of information transfer through social learning or teaching that influences behavior of individuals in a population
- Cultural transfer of information can alter behavioral phenotypes and influence the fitness of individuals

CONCEPT 51.3: Selection for individual survival and reproductive success can explain diverse behaviors

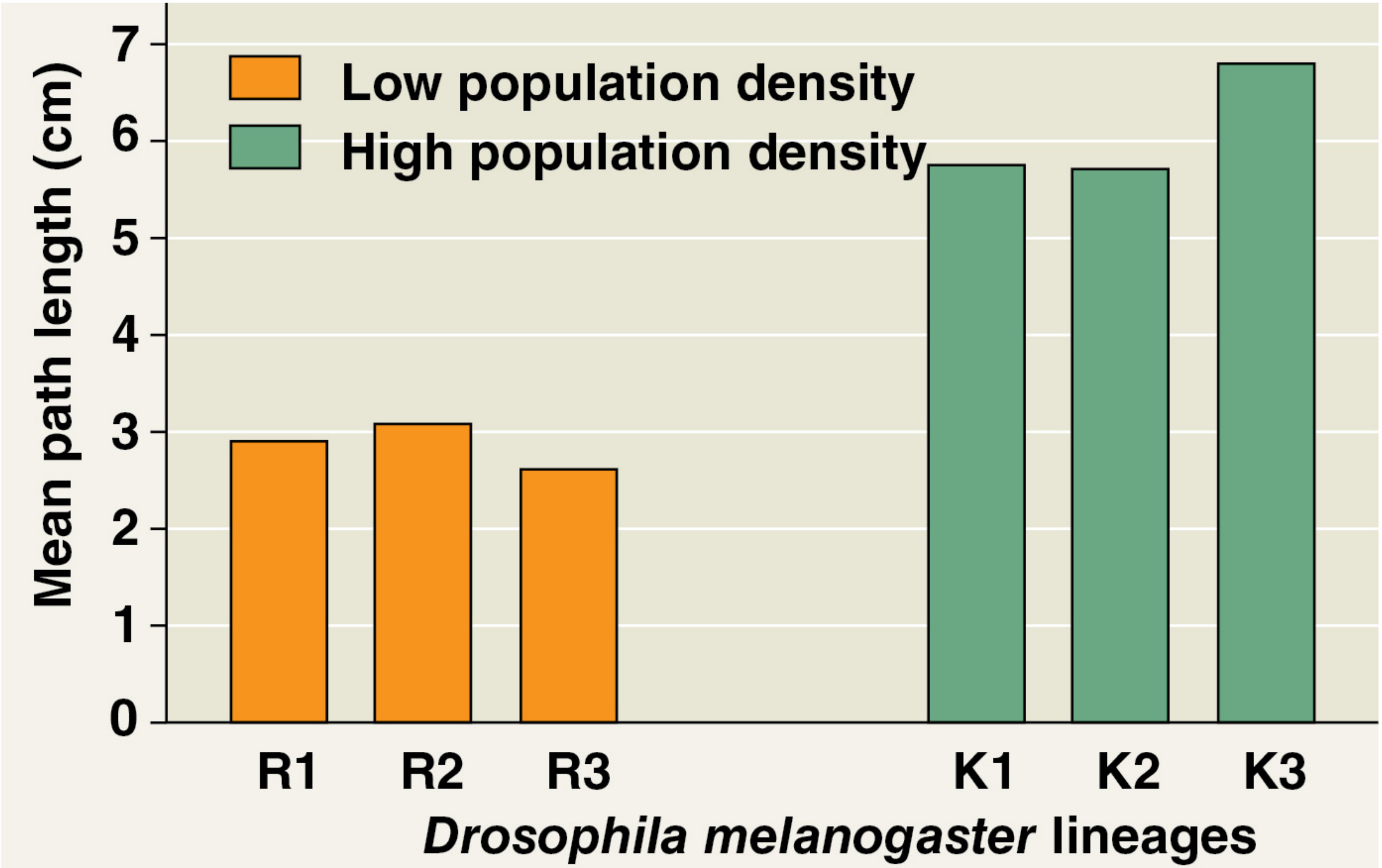
- **Foraging**, or food-obtaining behavior, includes recognizing, searching for, capturing, and eating food items

Evolution of Foraging Behavior

- In *Drosophila*, variation in a single gene called *forager* (*for*) dictates foraging behavior in the larvae
- Larvae with the for^R (“Rover”) allele travel farther while foraging than larvae with the for^S (“sitter”) allele
- Both alleles are present in natural populations
- Natural selection favors different alleles depending on the population density

- In populations kept at low density, larvae foraged over shorter distances than those at high density
- The *for*^{s} allele increased in frequency in low-density populations; the *for*^{R} allele increased in high density populations

Figure 51.13



Low population density
High population density
Mean path length (cm)
7
6
5
4
3
2
1
0
R1
R2
R3
K1
K2
K3
Drosophila melanogaster lineages

Optimal Foraging Model

- The **optimal foraging model** views foraging behavior as a compromise between the benefits of nutrition and the costs of obtaining food
- Costs of foraging include energy expenditure and the risk of being eaten while searching for food
- Natural selection should favor foraging behavior that minimizes the costs and maximizes the benefits

Balancing Risk and Reward

- As one of the most significant potential costs, predation risk has an influence on foraging behavior
  - For example, though food availability is somewhat lower, mule deer preferentially forage in open areas
  - The risk of predation by mountain lions is very high near forest edges, and much smaller in open areas

Mating Behavior and Mate Choice

- Mating behavior and mate choice play a major role in determining reproductive success
- Mating behavior includes seeking or attracting mates, choosing among potential mates, competing for mates, and caring for offspring

Mating Systems and Sexual Dimorphism

- The term mating system refers to the length and number of relationships between males and females
- In some species, mating is promiscuous, with no strong pair-bonds

- In some species, mates form a relationship of some duration that is **monogamous** (one male mates with one female)
- In species with monogamous mating systems, males and females look very similar to each other

(a) Monogamy

- In **polygamous** relationships, an individual of one sex mates with several individuals of the other sex
- Polygamous species are usually sexually dimorphic: Males and females differ in appearance

- In one form of polygamy, called polygyny, one male mates with many females
- In polygynous species, males are typically more showy and larger than the females

(b) Polygyny

- In another form of polygamy, called polyandry, one female mates with many males
- In polyandrous species, females are often more ornamented and may be larger than the males

Figure 51.14

(c) Polyandry

Figure 51.14

(a) Monogamy

(b) Polygyny

(c) Polyandry

Mating Systems and Parental Care

- The needs of the young are an important factor constraining evolution of mating systems
  - For example, most newly hatched birds need a large, continuous supply of food
  - In this case, males maximize reproductive success by helping one mate care for the offspring (monogamy)
  - If chicks can quickly care for themselves, males maximize reproductive success by seeking more mates (polygyny)

- Certainty of paternity also influences parental care and mating behavior
- A female can be certain that her eggs or young offspring contain her genes
- Even in monogamous relationships, some offspring may be fathered by a male other than the usual mate

- Paternal certainty is low in species with internal fertilization because mating and birth are separated over time
- Males may guard the females, remove sperm from the female reproductive tract, or produce large ejaculates to ensure paternity

- Certainty of paternity is 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

Figure 51.15

Sexual Selection and Mate Choice

- Sexual dimorphism results from sexual selection
- Sexual selection is a form of natural selection in which differences in reproductive success result from differences in mating success

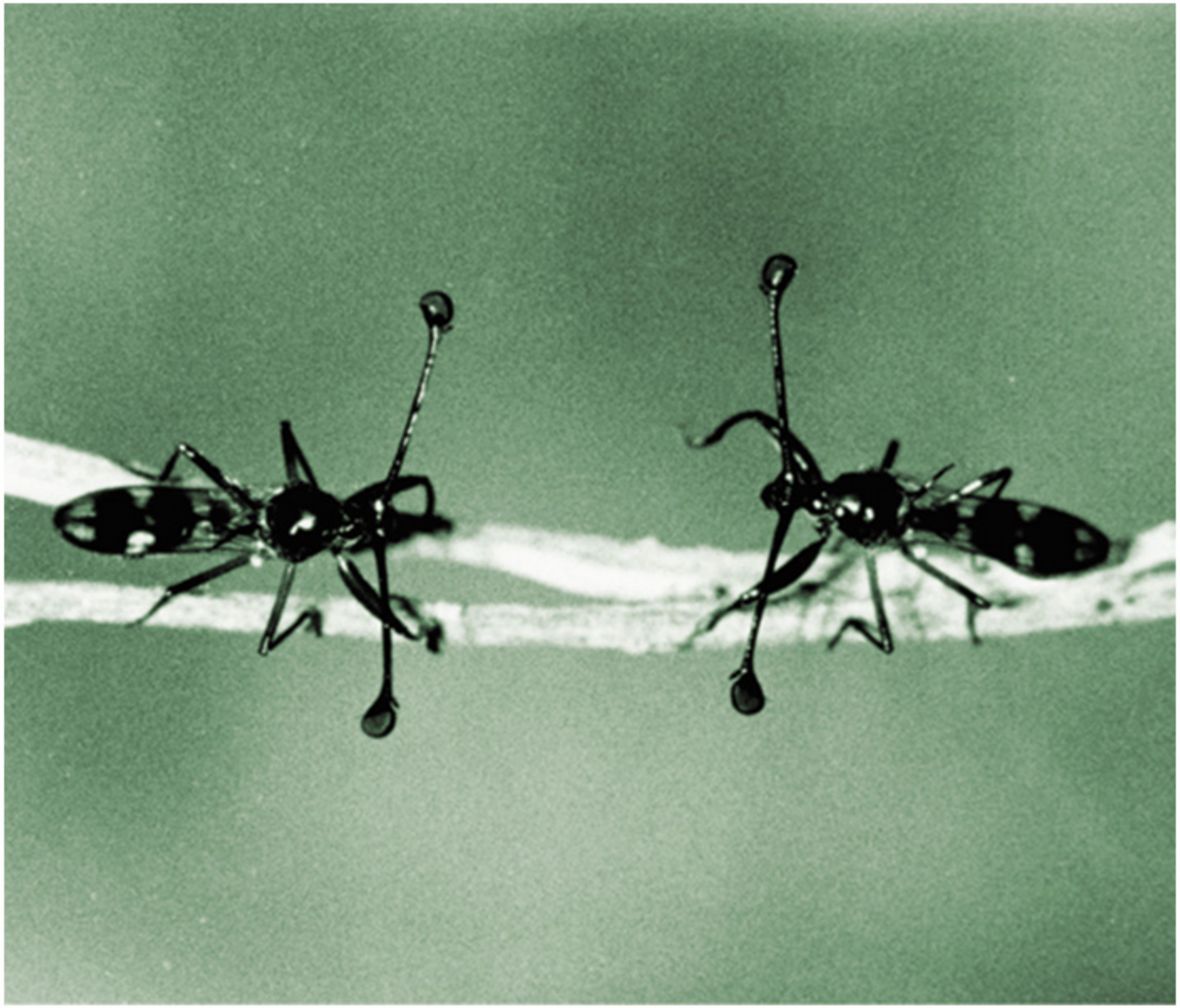
- In intersexual selection, members of one sex choose mates on the basis of certain traits
- Intrasexual selection involves competition between members of the same sex for mates

Mate Choice by Females

- Female choice is a type of intersexual selection
- Females drive sexual selection in males by choosing mates with specific behaviors or anatomical features
  - For example, female stalk-eyed flies are more likely to mate with males that have relatively long eyestalks

- Ornamentation, such as long eyestalks, correlate in general with health and vitality
- Females that select healthy mates are likely to produce more offspring that survive and reproduce
- Males may compete in ritualized contests to attract female attention

Figure 51.16

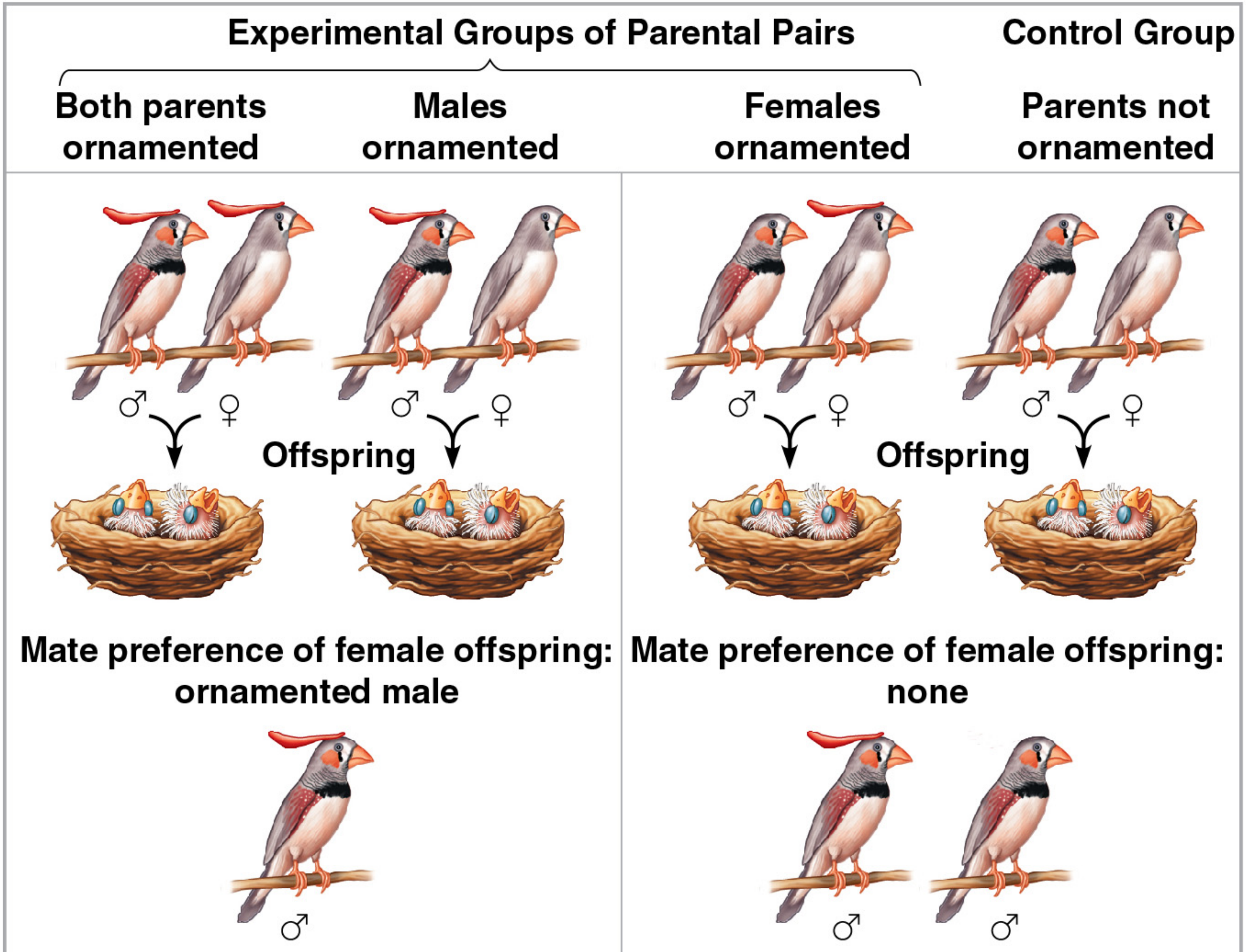


- Imprinting has been experimentally demonstrated to influence mate choice in zebra finches
- Both male and female zebra finches normally lack any feather crest on their head

Figure 51.17

- To simulate ornamentation, researchers taped a red feather to the foreheads of zebra finches
- Chicks were raised by all possible combinations of ornamented and unornamented parents

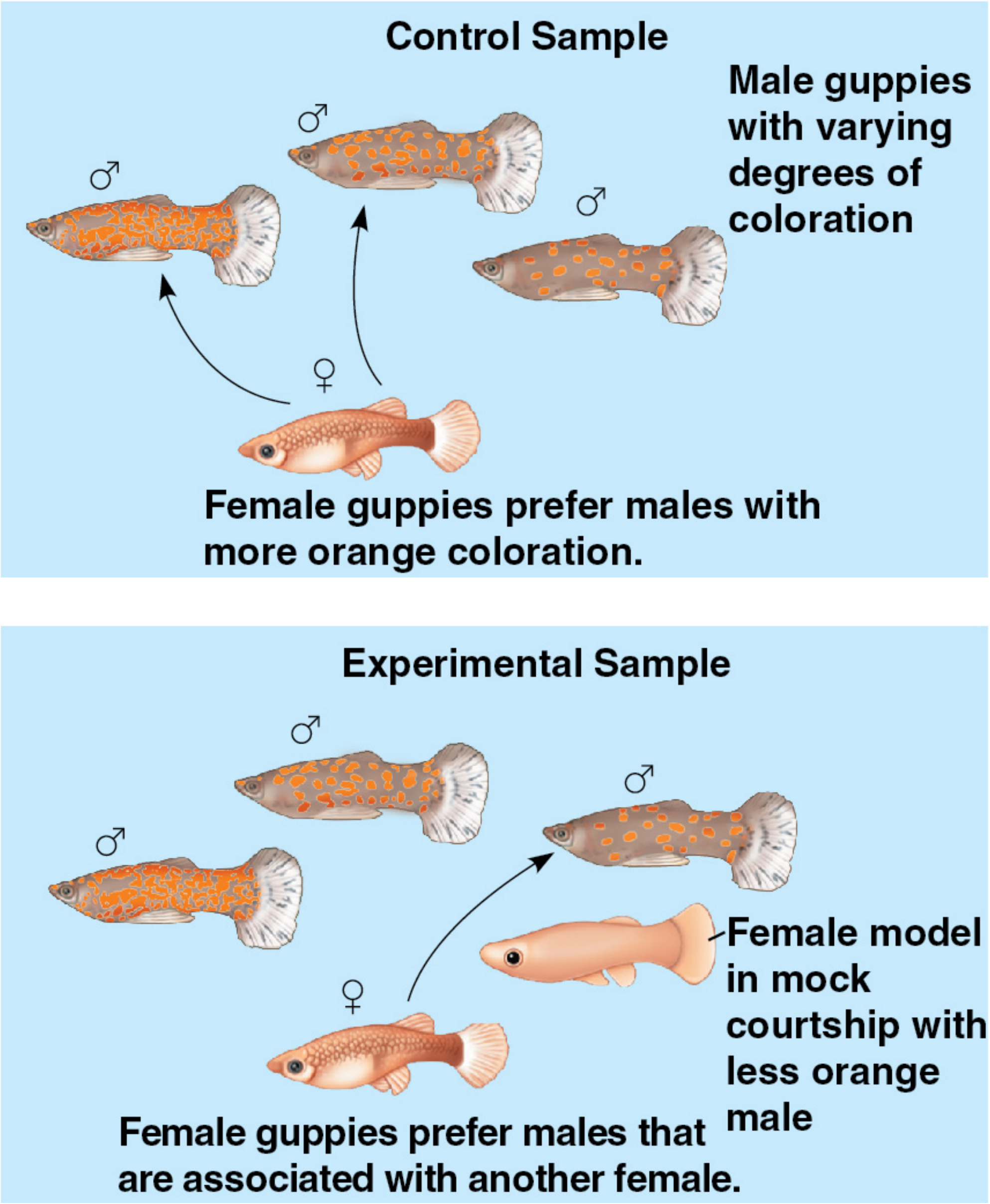
Figure 51.18


Experimental Groups of Parental Pairs
Control Group
Both parents ornamented
Males ornamented
Females ornamented
Parents not ornamented
♂
♀
Offspring
Mate preference of female offspring: ornamented male
Mate preference of female offspring: none

- Males showed no preference for ornamented mates
- Females raised by males without ornamentation also showed no mate preference
- Females raised by ornamented males showed a preference for ornamented males as their mates

- **Mate-choice copying** is a behavior in which individuals copy the mate choice of others
  - For example, if other females are not present, female guppies choose males with the most orange coloration
  - If a female model simulates courtship with a less orange male, females will chose that male instead
- This behavior may serve to increase the attractiveness of the offspring to the opposite sex

Figure 51.19



Control Sample
Male guppies with varying degrees of coloration
♂
♂
♂
♀
Female guppies prefer males with more orange coloration.
Experimental Sample
♂
♂
♂
♀
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 reduces variation among males
- It may involve agonistic behavior, a ritualized contest determining access to resources, such as mates

Figure 51.20

Video: Agonistic Behavior in Wolves

Video: Snake Ritual Wrestling

Applying Game Theory

- The fitness of a behavioral phenotype often depends on the other behavioral phenotypes in the population
- **Game theory** evaluates alternative strategies in situations where the outcome depends on the strategies of all individuals involved

- Game theory can be applied to mating behavior
  - For example, the common side-blotched lizard of California may have a blue, orange, or yellow throat
  - Orange-throat males are the most aggressive and defend large territories with many females
  - Blue-throats defend small territories with few females
  - Yellow-throats are nonterritorial, mimic females, and use “sneaky” strategies to mate

Figure 51.21

- Like rock-paper-scissors, each strategy outcompetes one and is outcompeted by the other strategy
- The success of each male lizard type depends on the relative abundance of the other types
- Frequency-dependent selection maintains all three types; the most prevalent type switches periodically

CONCEPT 51.4: Genetic analyses and the concept of inclusive fitness provide a basis for studying the evolution of behavior

- Genetic variation underlies the evolution of particular behaviors, such as “selfless” behavior

Genetic Basis of Behavior

- Master regulatory genes control behavior by directing the expression and activity of many genes
  - For example, the *fru* gene is a master regulatory gene that controls several genes involved in sex-specific development and courtship behavior in fruit flies

- Variation in the activity or amount of a gene product can have a large effect on behavior
  - For example, male prairie voles pair-bond with their mates and provide care to offspring, while male meadow voles do not
  - The expression of the receptor gene for **antidiuretic hormone (ADH)**, or **vasopressin**, determines which behavioral pattern develops

Figure 51.22

Genetic Variation and the Evolution of Behavior

- When behavioral variation between populations within a species correlates with environmental variation, it may reflect natural selection

Case Study: *Variation in Prey Selection*

- The natural diet of the western garter snake varies across its range in California
- Coastal populations feed mostly on banana slugs, whereas inland populations feed on other organisms
- Banana slugs are abundant in coastal areas, but are rare or absent in inland habitats
- When offered banana slugs, most coastal snakes ate them, whereas inland snakes refused them

Figure 51.23

- The taste for banana slugs has a genetic basis
- Pregnant snakes were collected from wild coastal and inland populations
- Most offspring of coastal mothers repeatedly ate banana slugs; most offspring of inland mothers refused to eat banana slugs even once

- The populations differ in ability to detect and respond to odor molecules produced by banana slugs
- A small frequency of the inland snakes that first colonized coastal habitats may have had this ability
- Over 10,000 years, natural selection favored coastal snakes that fed upon the abundant banana slugs

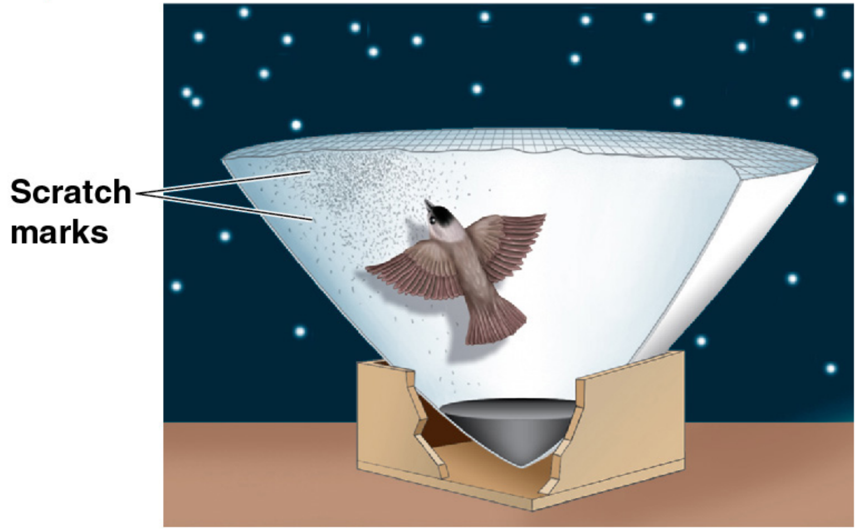
Case Study: *Variation in Migratory Patterns*

- Blackcaps are small, migratory warblers (birds)
- Most that breed in Germany migrate southwest to Spain and then south to spend winter in Africa
- Since the 1950's, many thousands have migrated westward from central Germany to winter in Britain

- Under laboratory conditions, each migratory population exhibits different migratory behaviors
- The migratory patterns—to the west or southwest—reflect genetic differences between the populations
- This heritable difference suggests the change in migration pattern resulted from natural selection

Figure 51.24

Experiment



Results

- The change in migratory behavior occurred recently and rapidly, from 1950 to the present
- Shorter distance and the abundance of winter bird feeders in Britain likely favored westward migrants

Altruism

- Natural selection favors behavior that maximizes an individual's survival and reproduction
- Such behaviors are typically selfish, but some animal behaviors appear to be selfless
- **Altruism** describes behaviors that reduce the actor's fitness but increase the fitness of other individuals

- Belding’s ground squirrels behave altruistically by making an alarm call when they spot a predator
- The call alerts others to retreat to their burrows, but also alerts the predator to the caller’s location
- Calling increases an individual’s risk of being killed

- Altruism is also observed in honeybee societies
- The sterile workers never reproduce themselves, but labor on behalf of a single fertile queen
- They also sacrifice their lives by stinging intruders to defend the hive

- Altruism is observed in naked mole rats, social rodents that live underground in parts of Africa
- Colonies can include up to 300 individuals, but only the queen reproduces with a few males, called kings
- Nonreproductive individuals may sacrifice their lives to protect the queen and kings from predators

Figure 51.25

Inclusive Fitness

- Close relatives share genes, and thus contribute to each other's genetic representation in the population
- **Inclusive fitness** accounts for the affect of both one's own offspring and aid given to enable close relatives to produce offspring
  - For example, an animal can increase its inclusive fitness by giving its life to aid its offspring or siblings

Hamilton's Rule and Kin Selection

- **Hamilton's rule** measures the effect of an altruistic act on fitness considering three key variables
  - Benefit (*B*), the number of extra offspring the recipient produces
  - Cost (*C*), how many fewer offspring the altruist produces
  - **Coefficient of relatedness** (*r*), the fraction of shared genes between the altruist and the recipient

- Hamilton's rule produces a formula that can be used to predict whether natural selection will favor altruism

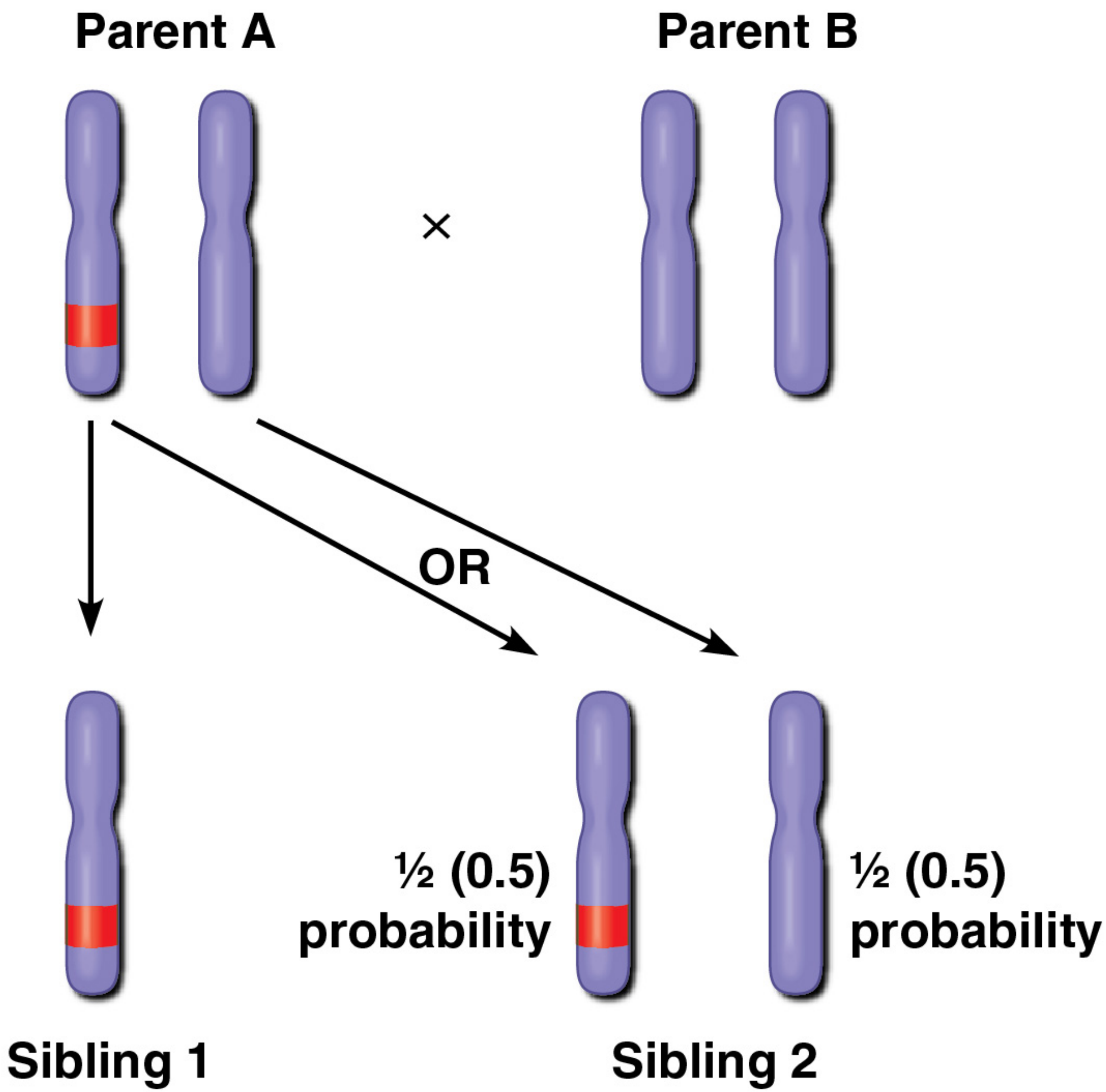
$$rB > C$$

- For example, Hamilton's rule can be used to predict if a girl should risk her life to save her young brother

- Assuming the average individual has two children, as a result of the girl's action
  - B = 2, her brother fathers two children
  - C = 0.25 × 2 = 0.5, the girl has a 25% chance of dying and not having two children
  - r = 0.5, on average, siblings share half their genes

- The coefficient of relatedness between siblings can be seen in terms of the separation of homologous chromosomes during meiosis

Figure 51.26


Parent A
Parent B
×
OR
½ (0.5) probability
½ (0.5) probability
Sibling 1
Sibling 2

- If the girl saves her brother

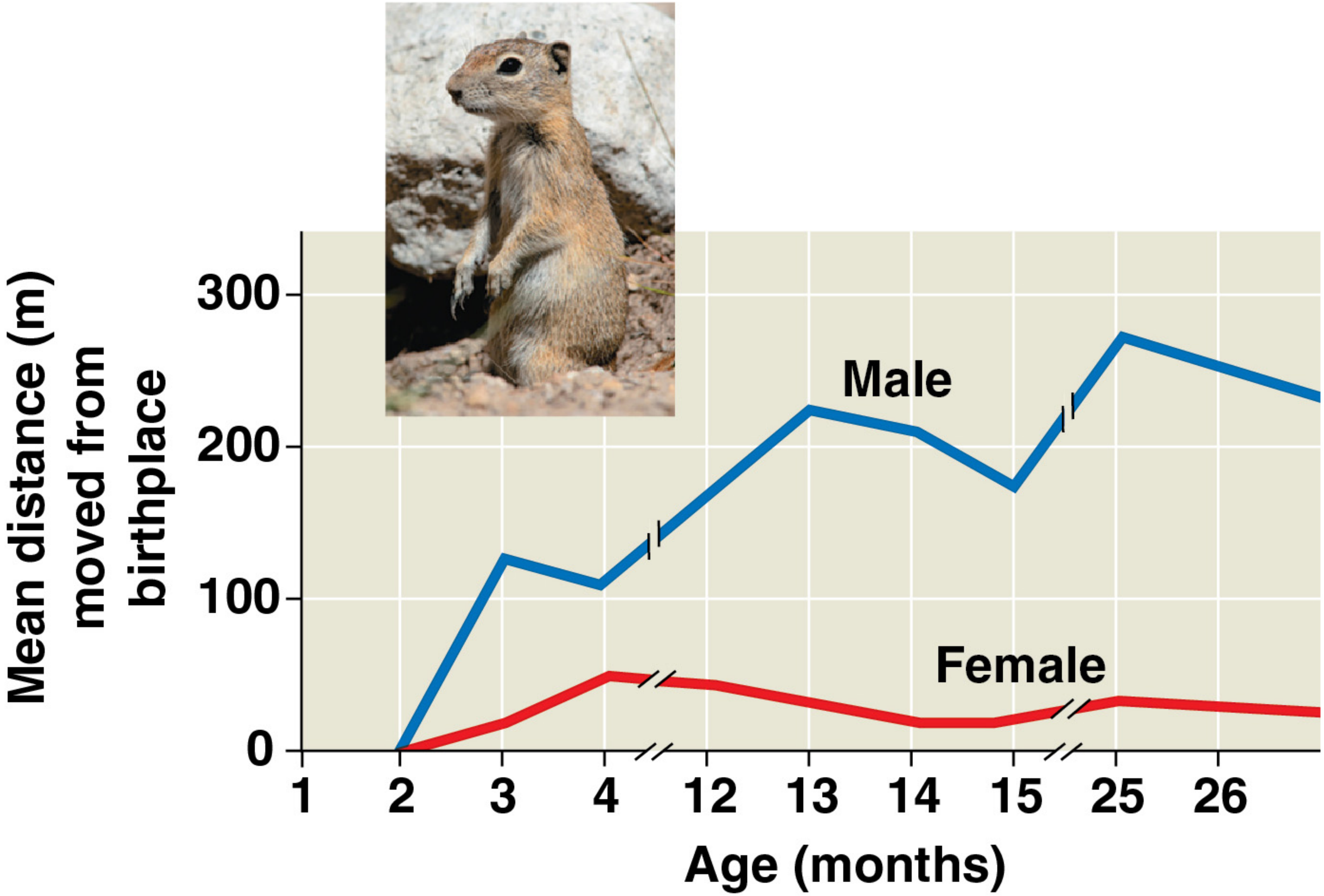
$$rB = 1 > C = 0.5$$

- Hamilton's rule predicts that the girl will maximize her inclusive fitness by risking her life to save her brother
- Natural selection should favor this altruistic act

- **Kin selection** favors altruistic behavior by enhancing the reproductive success of relatives
- Kin selection weakens as the relatedness between individuals decreases
  - *r* = 0.5 between siblings
  - *r* = 0.25 between an aunt and her niece or nephew
  - *r* = 0.125 between first cousins

- Alarm calling in Belding's ground squirrels shows the relationship between kin selection and altruism
  - Females settle close to their site of birth, whereas males settle at distant sites
  - Most alarm calls are given by females, who are likely aiding close relatives

Figure 51.27


Mean distance (m) moved from birthplace
300
200
100
0
Male
Female
1
2
3
4
12
13
14
15
25
26
Age (months)

- DNA analysis indicates that naked mole rats living within a colony are closely related
- Nonreproductive individuals increase their inclusive fitness by helping the reproductive queen and kings pass their genes to the next generation

Reciprocal Altruism

- Altruistic behavior toward unrelated individuals can be adaptive if the favor is returned in the future
- This type of altruism is called **reciprocal altruism**
- It is limited to species with stable social groups where individuals meet repeatedly and cheaters (who don't reciprocate) are punished

- The evolution of reciprocal altruism can be explained by the tit-for-tat behavioral strategy
- The rules of this strategy always favor cooperation, unless an opponent cheated in the last interaction
- This provides a mechanism for punishing cheaters
- Individuals return to cooperative behavior as soon as the cheating individual becomes cooperative

Evolution and Human Culture

- Due to our marked capacity for learning, humans are probably more able than any other animal to acquire new behaviors and skills

Figure 51.28

- Human behavior and culture are related to evolutionary theory in the discipline of sociobiology
- Human behavior results from interaction between genes and environment
- Our complex social and cultural institutions are a major distinction between humans and other animals

Figure 51.UN03

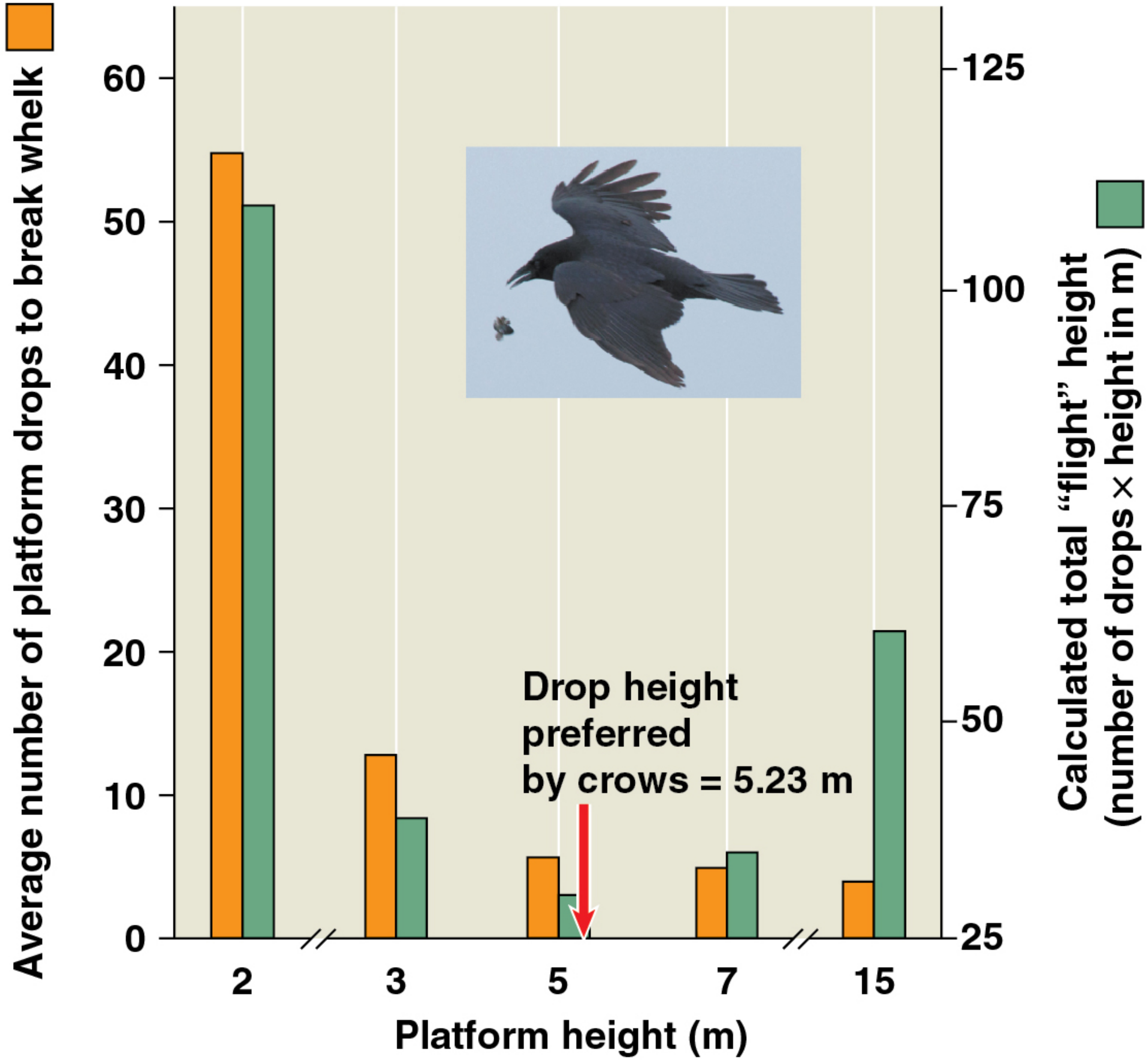


Figure 51.UN04

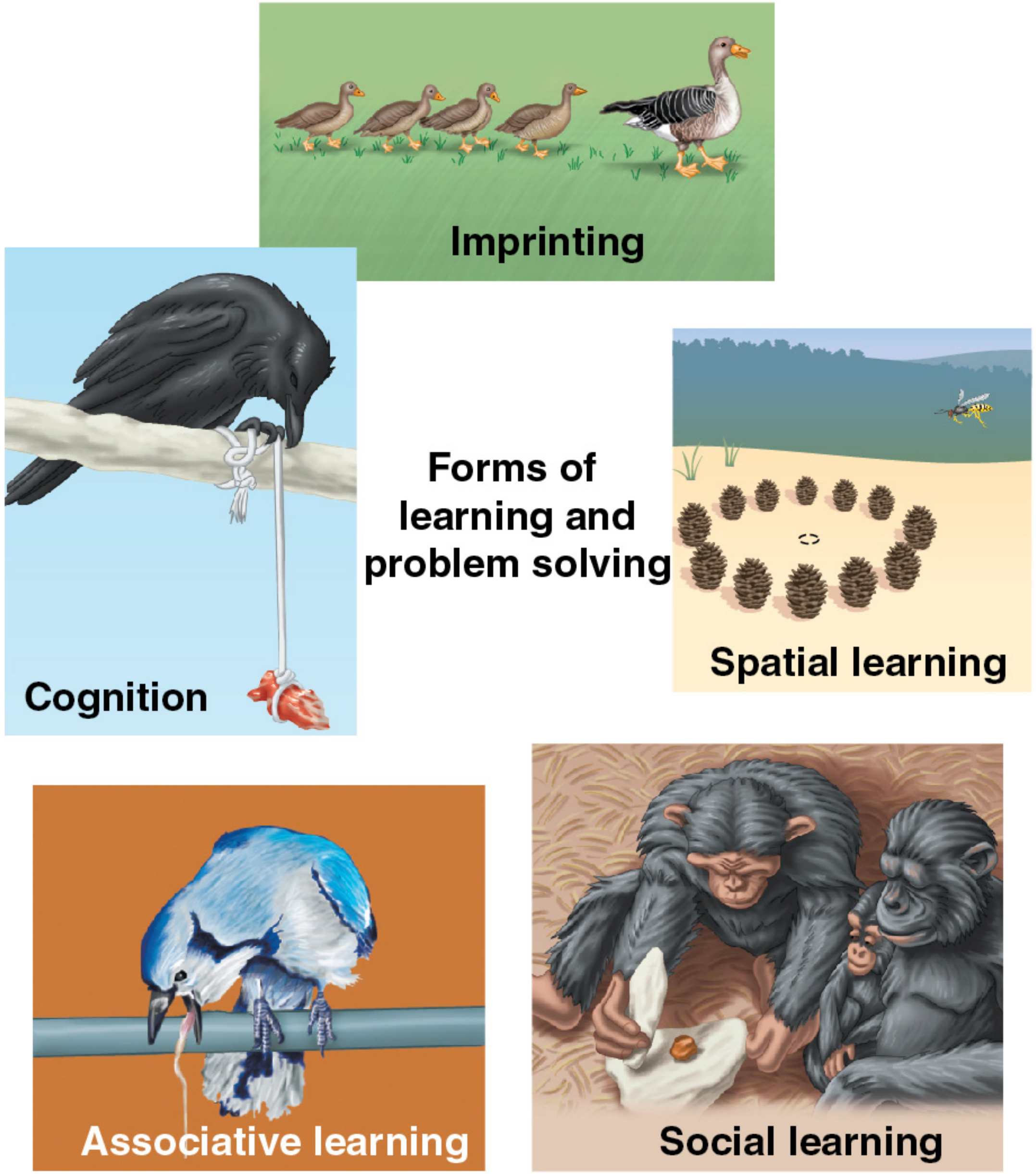


Figure 51.UN05