LECTURE PRESENTATIONS

For CAMPBELL BIOLOGY, NINTH EDITION

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Chapter 51

Animal Behavior

Lectures by
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Overview: The How and Why of Animal Activity

- Fiddler crabs feed with their small claw and wave their large claw
- Why do male fiddler crabs engage in claw waving behavior?
- Claw waving is used to repel other males and to attract females

Figure 51.1

- A **behavior** is the nervous system's response to a stimulus and is carried out by the muscular or the hormonal system
- Behavior is subject to natural selection

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

- Niko Tinbergen identified four questions that should be asked about animal behavior
  1. What stimulus elicits the behavior, and what physiological mechanisms mediate the response?
  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?

- **Behavioral ecology** is the study of the ecological and evolutionary basis for animal behavior

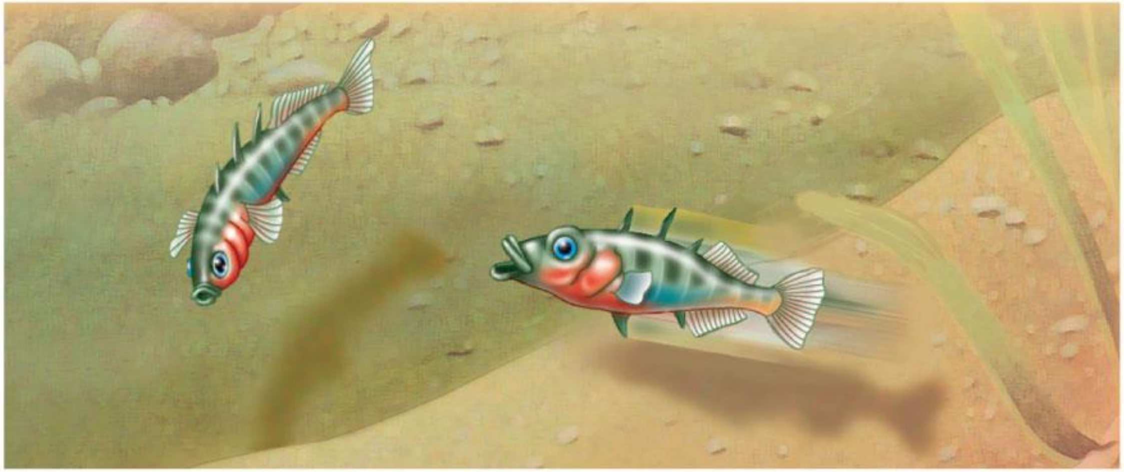
- Behavioral ecology integrates proximate and ultimate explanations for animal behavior
- Proximate causation addresses “how” a behavior occurs or is modified, including Tinbergen’s questions 1 and 2
- Ultimate causation addresses “why” a behavior occurs in the context of natural selection, including Tinbergen’s questions 3 and 4

Fixed Action Patterns

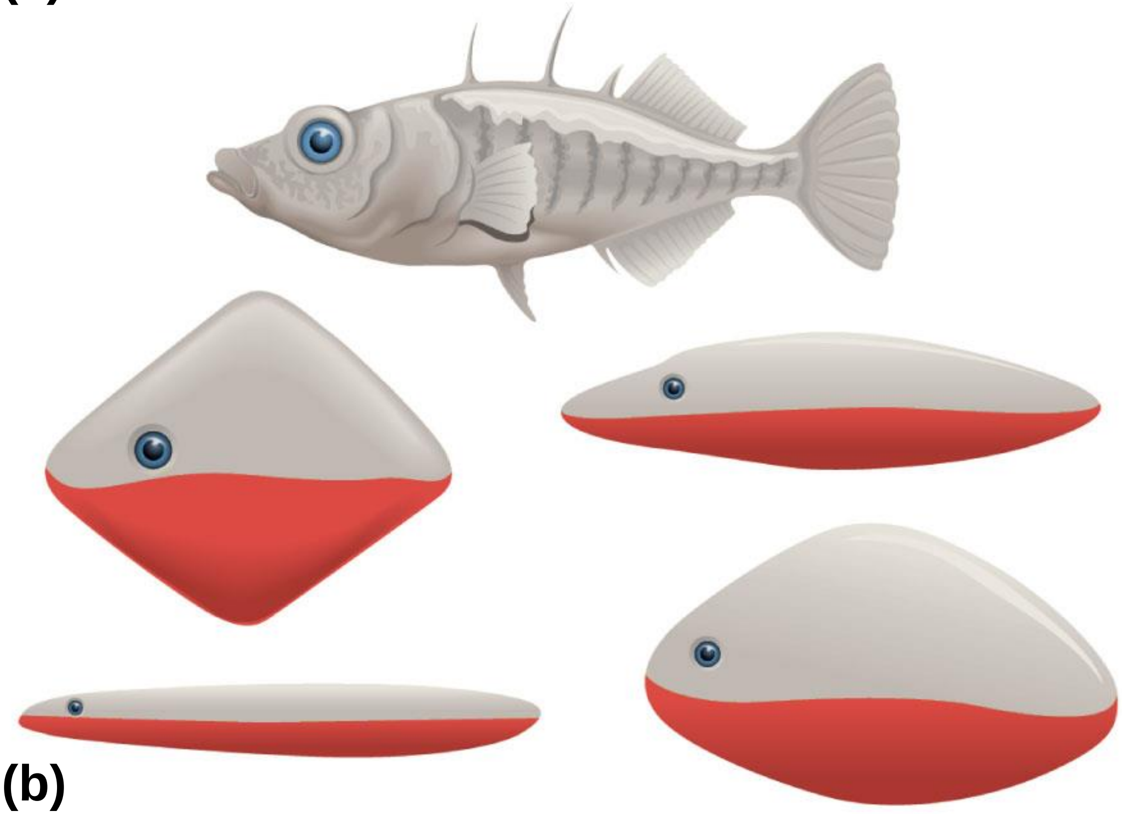
- A **fixed action pattern** is a sequence of unlearned, innate behaviors that is unchangeable
- Once initiated, it is usually carried to completion
- A fixed action pattern is triggered by an external cue known as a **sign stimulus**

- Tinbergen observed male stickleback fish responding to a passing red truck
- In male stickleback fish, the stimulus for attack behavior is the red underside of an intruder
- When presented with unrealistic models, the attack behavior occurs as long as some red is present

Figure 51.2



(a)



(b)

Migration

- Environmental cues can trigger movement in a particular direction
- **Migration** is a regular, long-distance change in location
- Animals can orient themselves using
  - The position of the sun and their circadian clock, an internal 24-hour clock that is an integral part of their nervous system
  - The position of the North Star
  - The Earth's magnetic field

Figure 51.3

Behavioral Rhythms

- Some animal behavior is affected by the animal's circadian rhythm, a daily cycle of rest and activity
- Behaviors such as migration and reproduction are linked to changing seasons, or a circannual rhythm
- Daylight and darkness are common seasonal cues
- Some behaviors are linked to lunar cycles, which affect tidal movements

Animal Signals and Communication

- In behavioral ecology, a **signal** is a behavior that causes a change in another animal's behavior
- **Communication** is the transmission and reception of signals

Forms of Animal Communication

- Animals communicate using visual, chemical, tactile, and auditory signals
- Fruit fly courtship follows a three step stimulus-response chain

1. A male identifies a female of the same species and orients toward her

- Chemical communication: he smells a female’s chemicals in the air
- Visual communication: he sees the female and orients his body toward hers

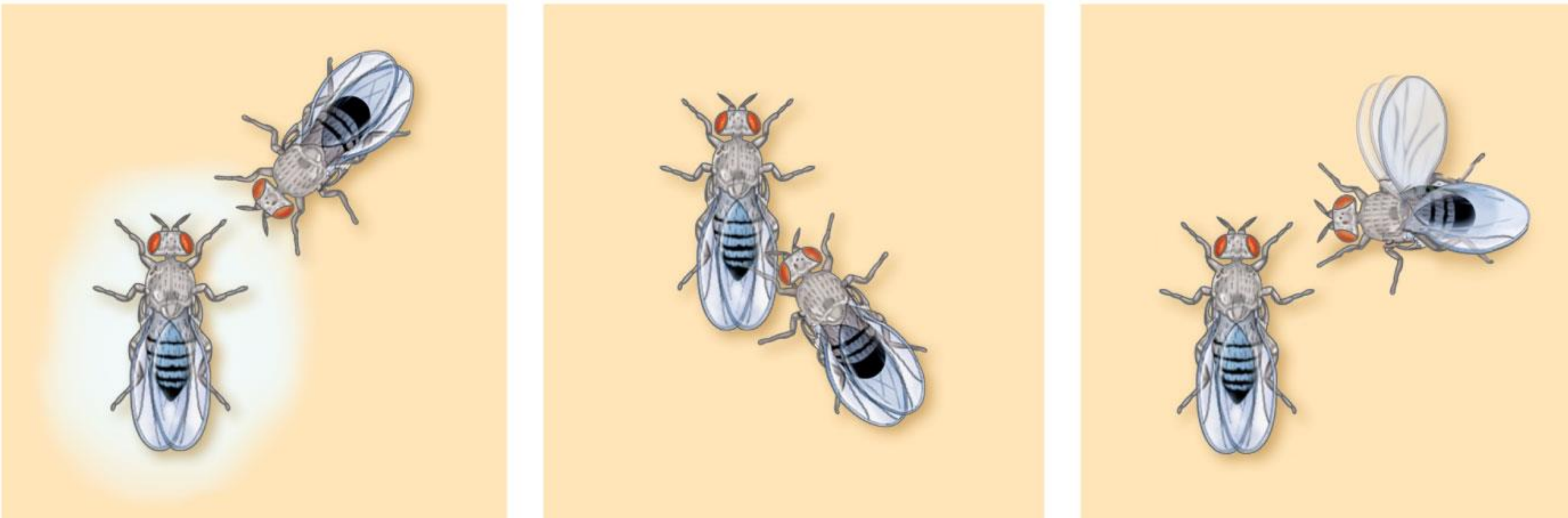
2. The male alerts the female to his presence

- 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 to inform the female of his species

- Auditory communication: he extends and vibrates his wing
- If all three steps are successful, the female will allow the male to copulate

Figure 51.4

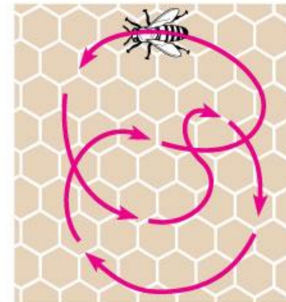


(a) Orienting (b) Tapping (c) “Singing”

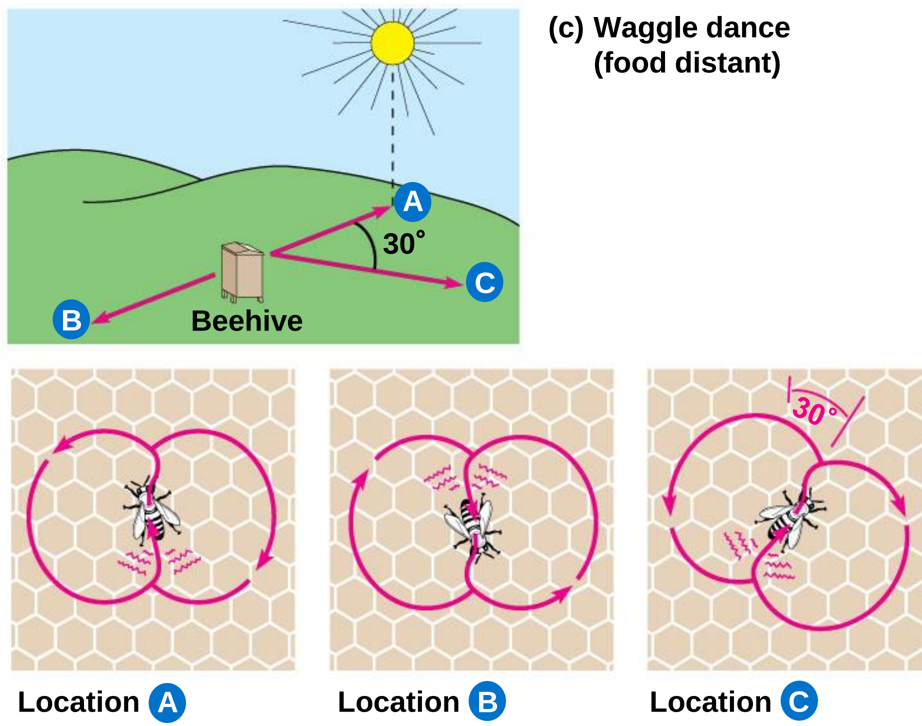
- Honeybees show complex communication with symbolic language
- A bee returning from the field performs a dance to communicate information about the distance and direction of a food source

Figure 51.5

(a) Worker bees



(b) Round dance (food near)



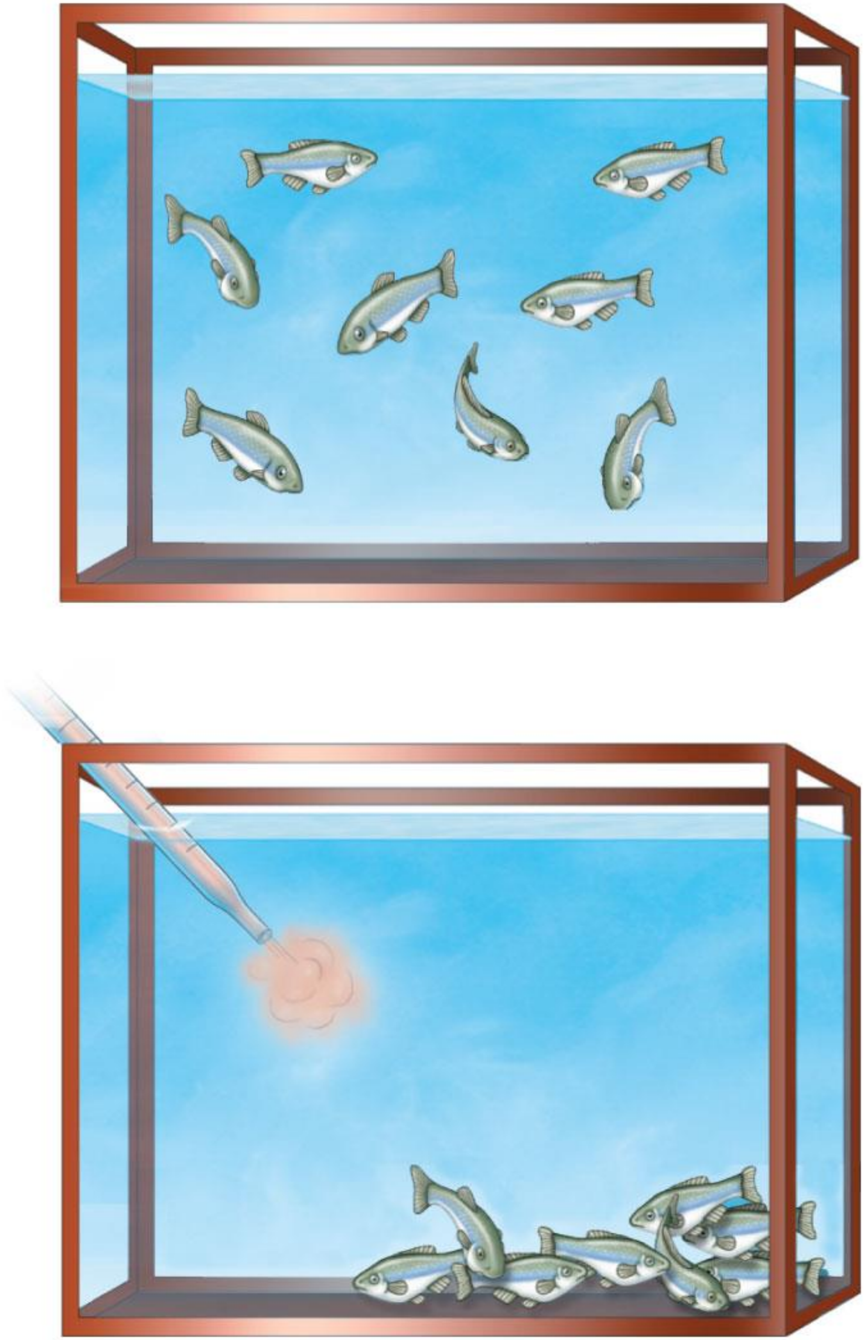
(c) Waggle dance (food distant)

Pheromones

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

- For example,
  - A female moth can attract a male moth several kilometers distant
  - A honeybee queen produces a pheromone that affects the development and behavior of female workers and male drones
  - 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

Figure 51.6



(a) Minnows before alarm

(b) Minnows after alarm

- Pheromones can be effective at very low concentrations
- Nocturnal animals, such as most terrestrial mammals, depend on olfactory and auditory communication
- Diurnal animals, such as humans and most birds, use visual and auditory communication

Concept 51.2: Learning establishes specific links between experience and behavior

- **Innate behavior** is developmentally fixed and does not vary among individuals

Experience and Behavior

- Cross-fostering studies help behavioral ecologists to identify the contribution of environment to an animal's behavior
- A **cross-fostering study** places the young from one species in the care of adults from another species

- Studies of California mice and white-footed mice have uncovered an influence of social environment on aggressive and parental behaviors
- Cross-fostered mice developed some behaviors that were consistent with their foster parents

Table 51.1

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.

- In humans, **twin studies** allow researchers to compare the relative influences of genetics and environment on behavior

Learning

- **Learning** is the modification of behavior based on specific experiences

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
- The imprint stimulus in greylag geese is a nearby object that is moving away from the young geese

Figure 51.7

(a) Konrad Lorenz and geese

(b) Pilot and cranes

- Conservation biologists have taken advantage of imprinting in programs to save the whooping crane from extinction
- Young whooping cranes can imprint on humans in “crane suits” who then lead crane migrations using ultralight aircraft

Figure 51.7b

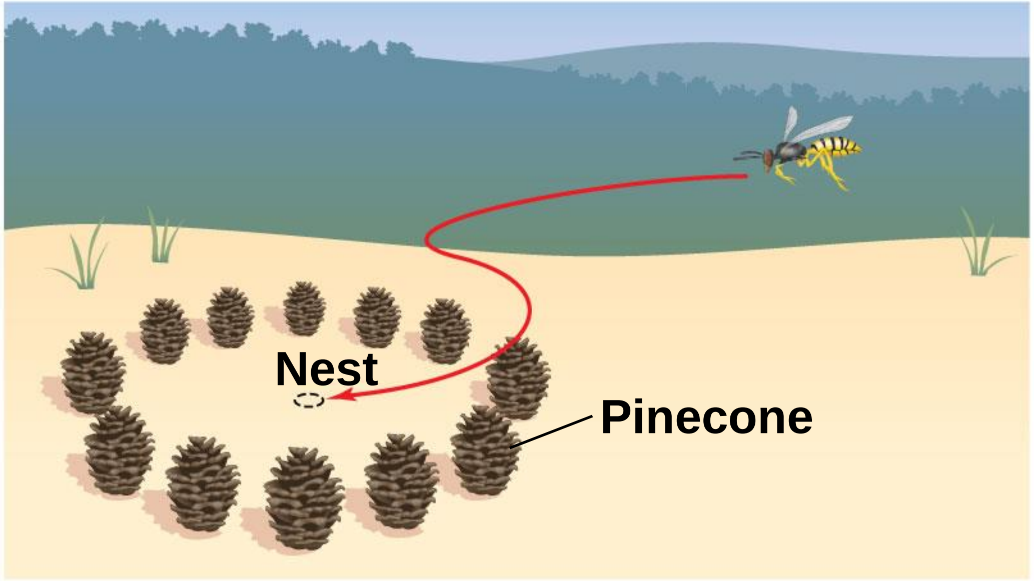
(b) Pilot and cranes

Spatial Learning and Cognitive Maps

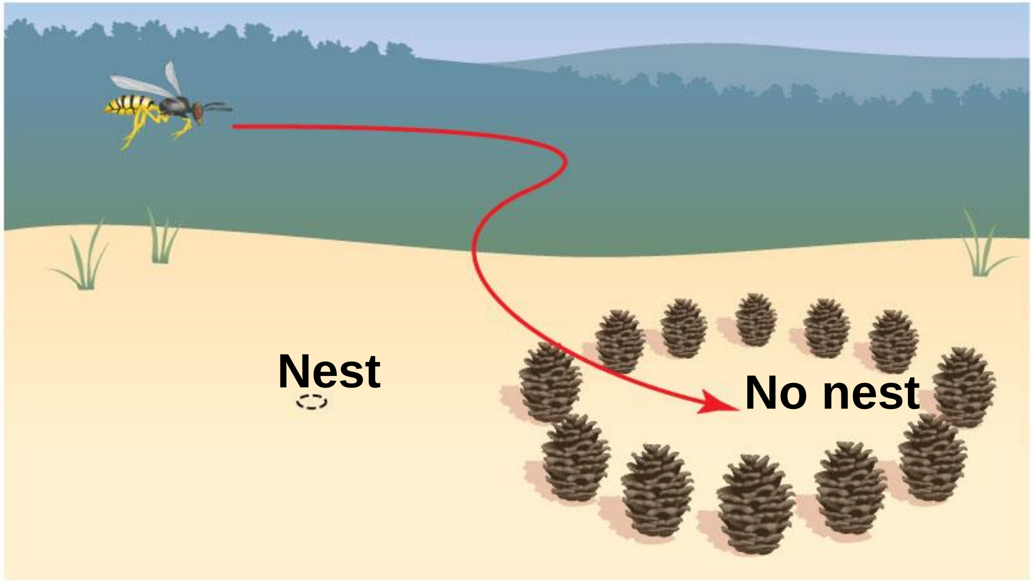
- **Spatial learning** is a more complex modification of behavior based on experience with the spatial structure of the environment
- Niko Tinbergen showed how digger wasps use landmarks to find nest entrances

Figure 51.8

EXPERIMENT



RESULTS



- A **cognitive map** is an internal representation of spatial relationships between objects in an animal's surroundings
  - For example, Clark's nutcrackers can find food hidden in caches located halfway between particular landmarks

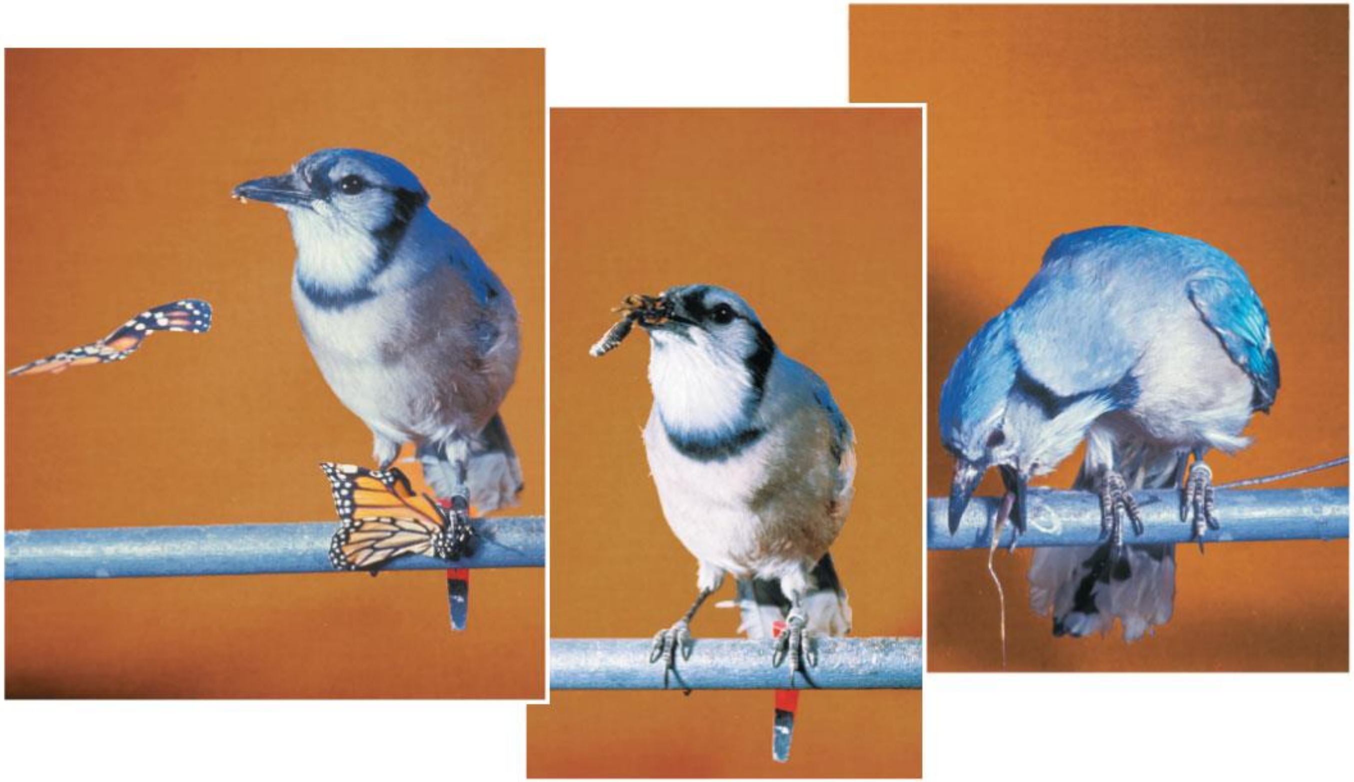
Associative Learning

- In **associative learning**, animals associate one feature of their environment with another
  - For example, a white-footed mouse will avoid eating caterpillars with specific colors after a bad experience with a distasteful monarch butterfly caterpillar

- 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 anticipation at the bell's sound

- 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
  - For example, a predator may learn to avoid a specific type of prey associated with a painful experience

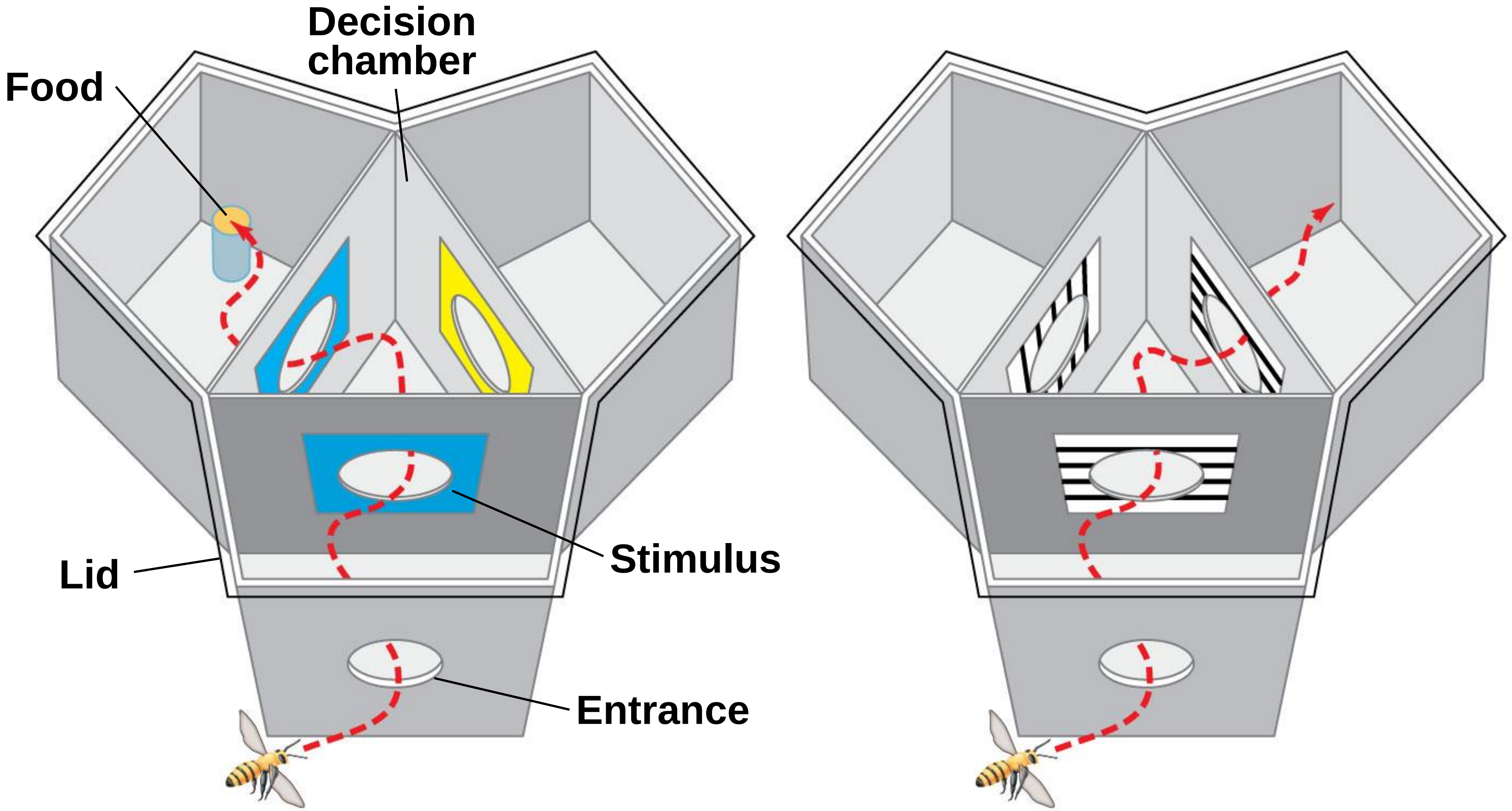
Figure 51.9



Cognition and Problem Solving

- **Cognition** is a process of knowing that may include awareness, reasoning, recollection, and judgment
  - For example, honeybees can distinguish “same” from “different”

Figure 51.10



(a) Color maze

(b) Pattern maze

- **Problem solving** is the process of devising a strategy to overcome an obstacle
  - For example, chimpanzees can stack boxes in order to reach suspended food
  - For example, ravens obtained food suspended from a branch by a string by pulling up the string

Development of Learned Behaviors

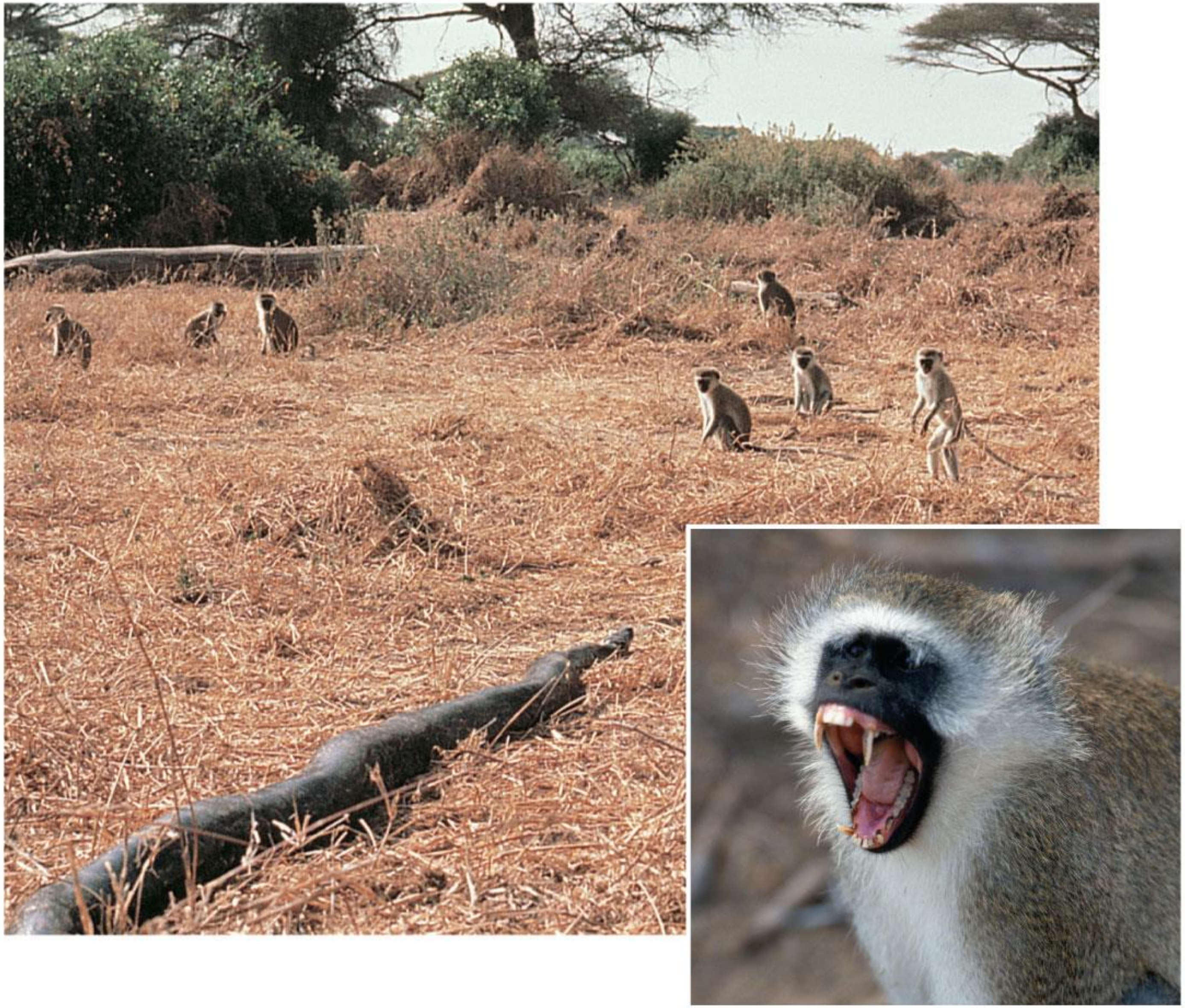
- Development of some behaviors occurs in distinct stages
  - For example a white-crowned sparrow memorizes the song of its species during an early sensitive period
  - The bird then learns to sing the song during a second learning phase

Social Learning

- **Social learning** is learning through the observation of others and 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

Figure 51.11

Figure 51.12



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

Concept 51.3: Selection for individual survival and reproductive success can explain most behaviors

- Behavior enhances survival and reproductive success in a population

Foraging Behavior

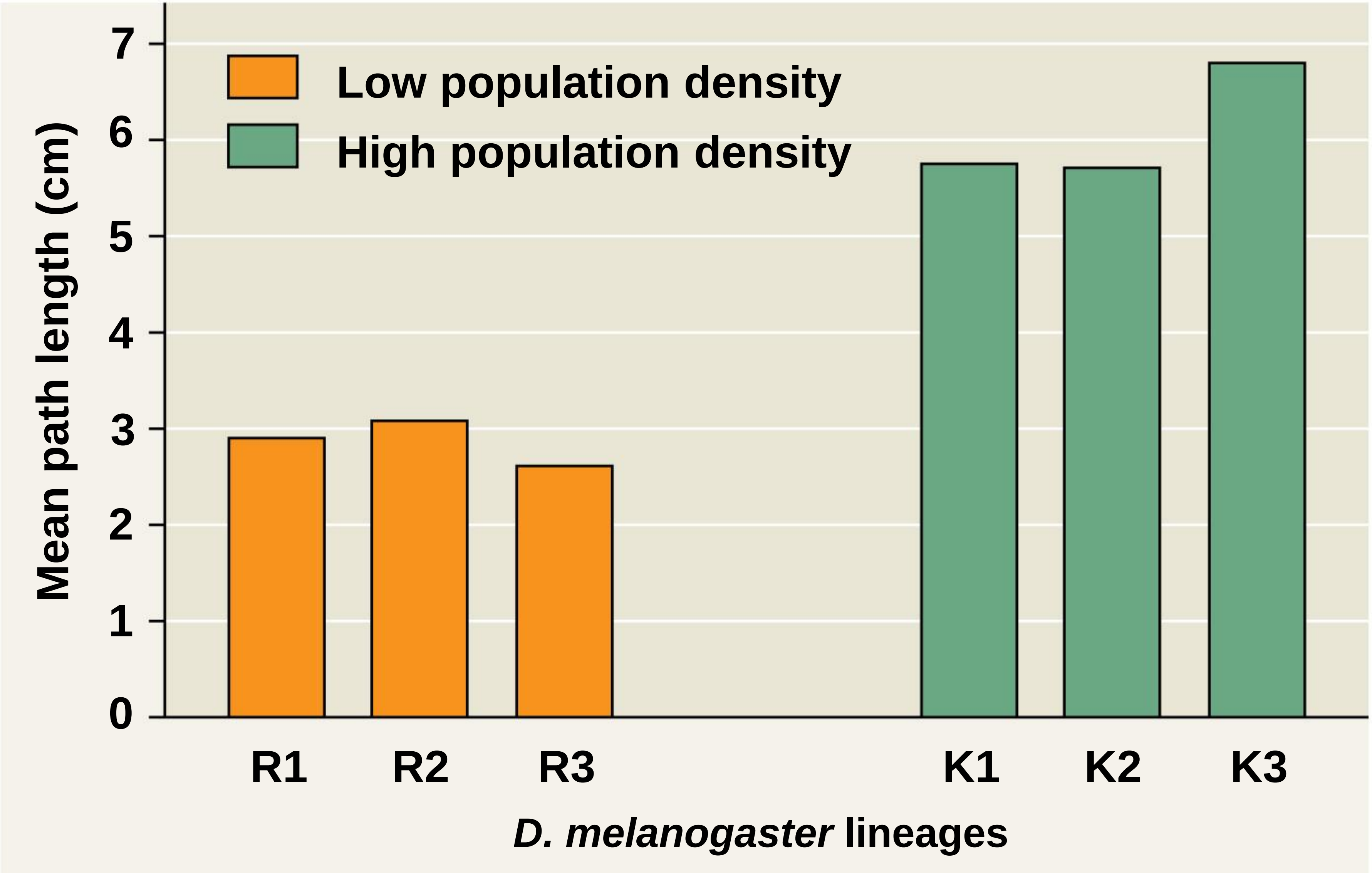
- Natural selection refines behaviors that enhance the efficiency of feeding
- **Foraging**, or food-obtaining behavior, includes recognizing, searching for, capturing, and eating food items

Evolution of Foraging Behavior

- In *Drosophila melanogaster*, variation in a gene dictates foraging behavior in the larvae
- Larvae with one allele travel farther while foraging than larvae with the other allele
- Larvae in high-density populations benefit from foraging farther for food, while 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

Figure 51.13


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

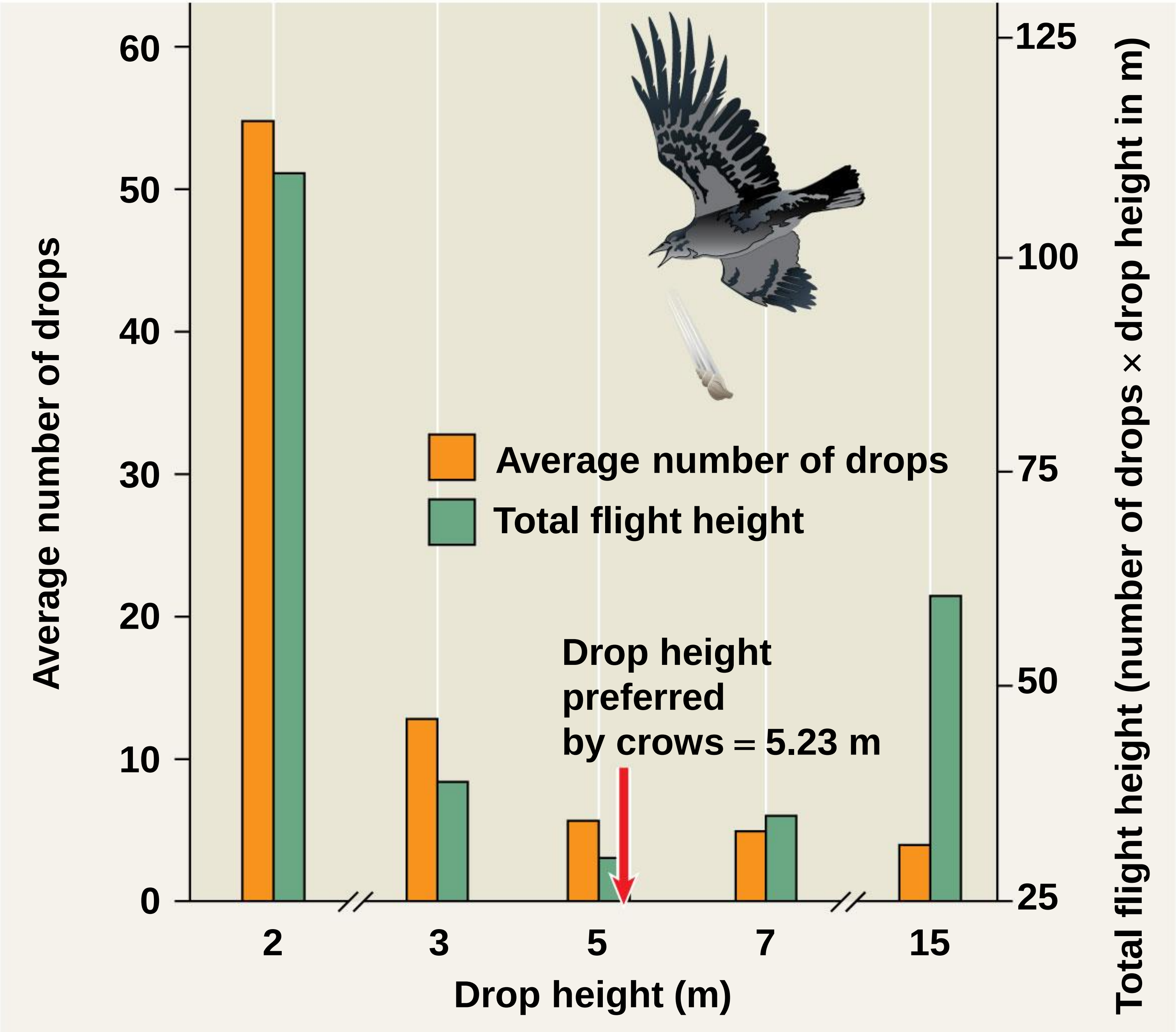
Optimal Foraging Model

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

- Optimal foraging behavior is demonstrated by the Northwestern crow
- A crow will drop a whelk (a mollusc) from a height to break its shell and feed on the soft parts
- The crow faces a trade-off between the height from which it drops the whelk and the number of times it must drop the whelk

- Researchers determined experimentally that the total flight height (which reflects total energy expenditure) was minimized at a drop height of 5 m
- The average flight height for crows is 5.23 m

Figure 51.14



60
50
40
30
20
10
0
Average number of drops
125
100
75
50
25
Total flight height (number of drops × drop height in m)
Average number of drops
Total flight height
Drop height
preferred
by crows = 5.23 m
2
3
5
7
15
Drop height (m)

Balancing Risk and Reward

- Risk of predation affects foraging behavior
  - For example, mule deer are more likely to feed in open forested areas where they are less likely to be killed by mountain lions

Mating Behavior and Mate Choice

- Mating behavior includes seeking or attracting mates, choosing among potential mates, competing for mates, and caring for offspring
- Mating relationships define a number of distinct mating systems

Mating Systems and Sexual Dimorphism

- 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
- Males and females with monogamous mating systems have similar external morphologies

Figure 51.15

(a) Monogamous species

(b) Polygynous species

(c) Polyandrous species

- 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
- 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

Figure 51.15b

(b) Polygynous species

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

Figure 51.15c

(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
  - 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

Figure 51.16

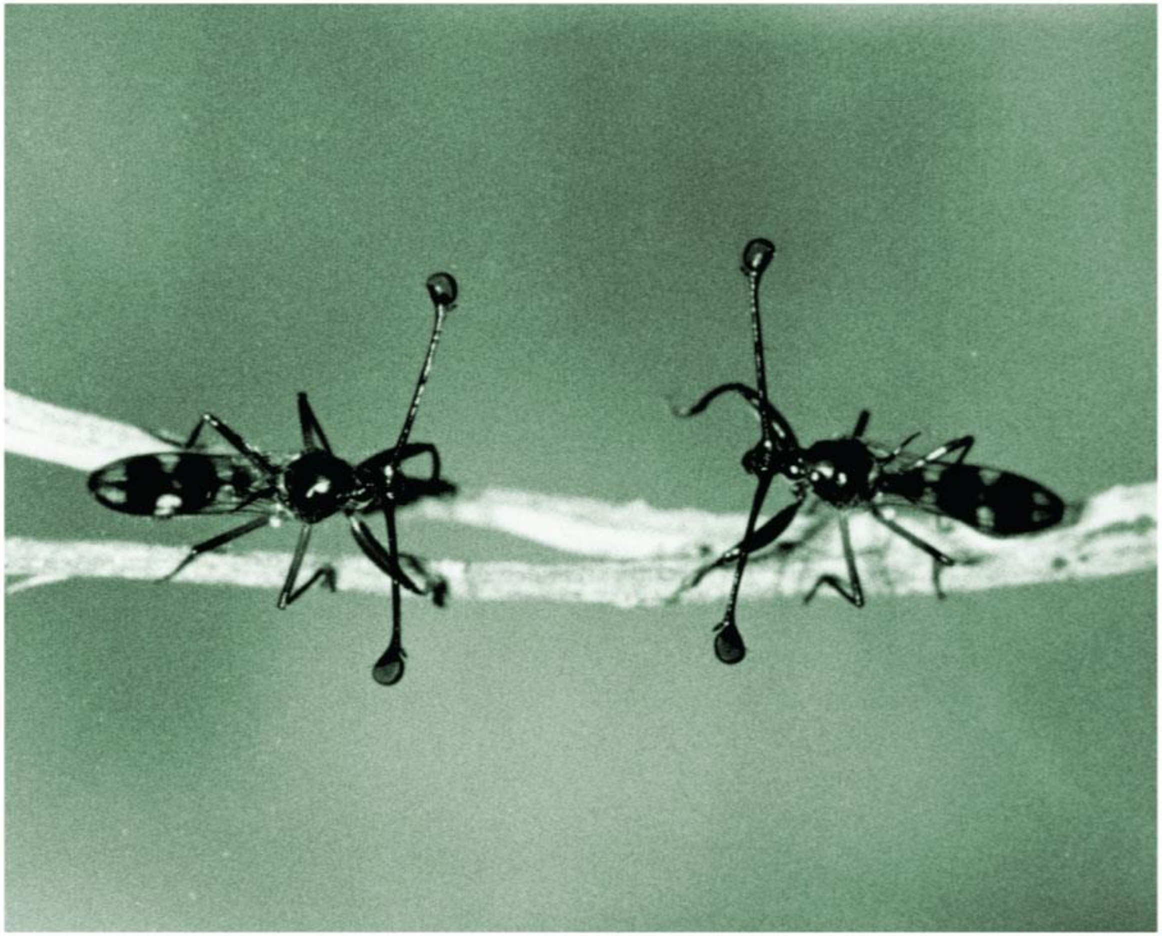
Sexual Selection and Mate Choice

- 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 drive sexual selection by choosing males with specific behaviors or features of anatomy
  - For example, female stalk-eyed flies choose males with relatively long eyestalks
- Ornaments, such as long eyestalks, often correlate with health and vitality

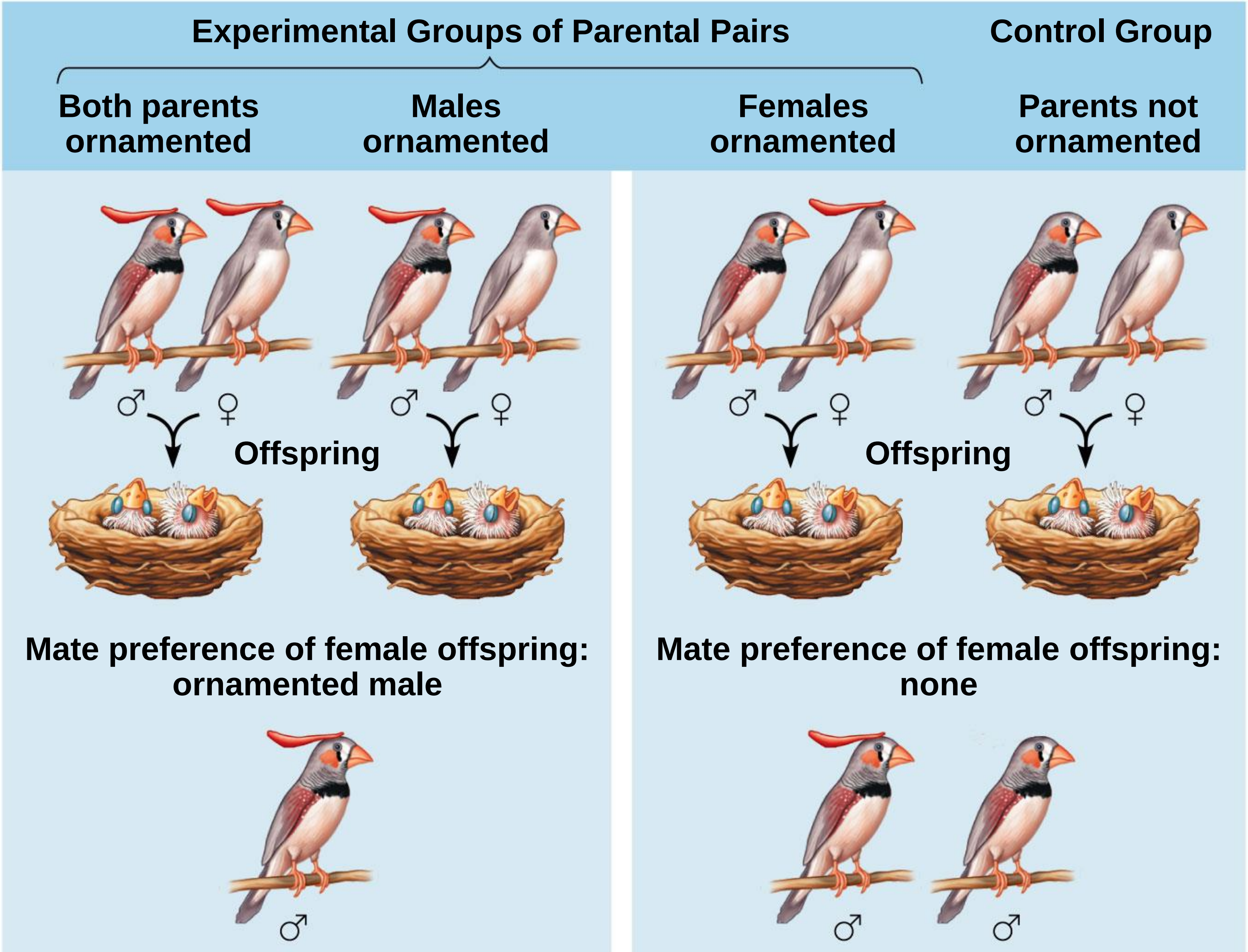
Figure 51.17



- 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

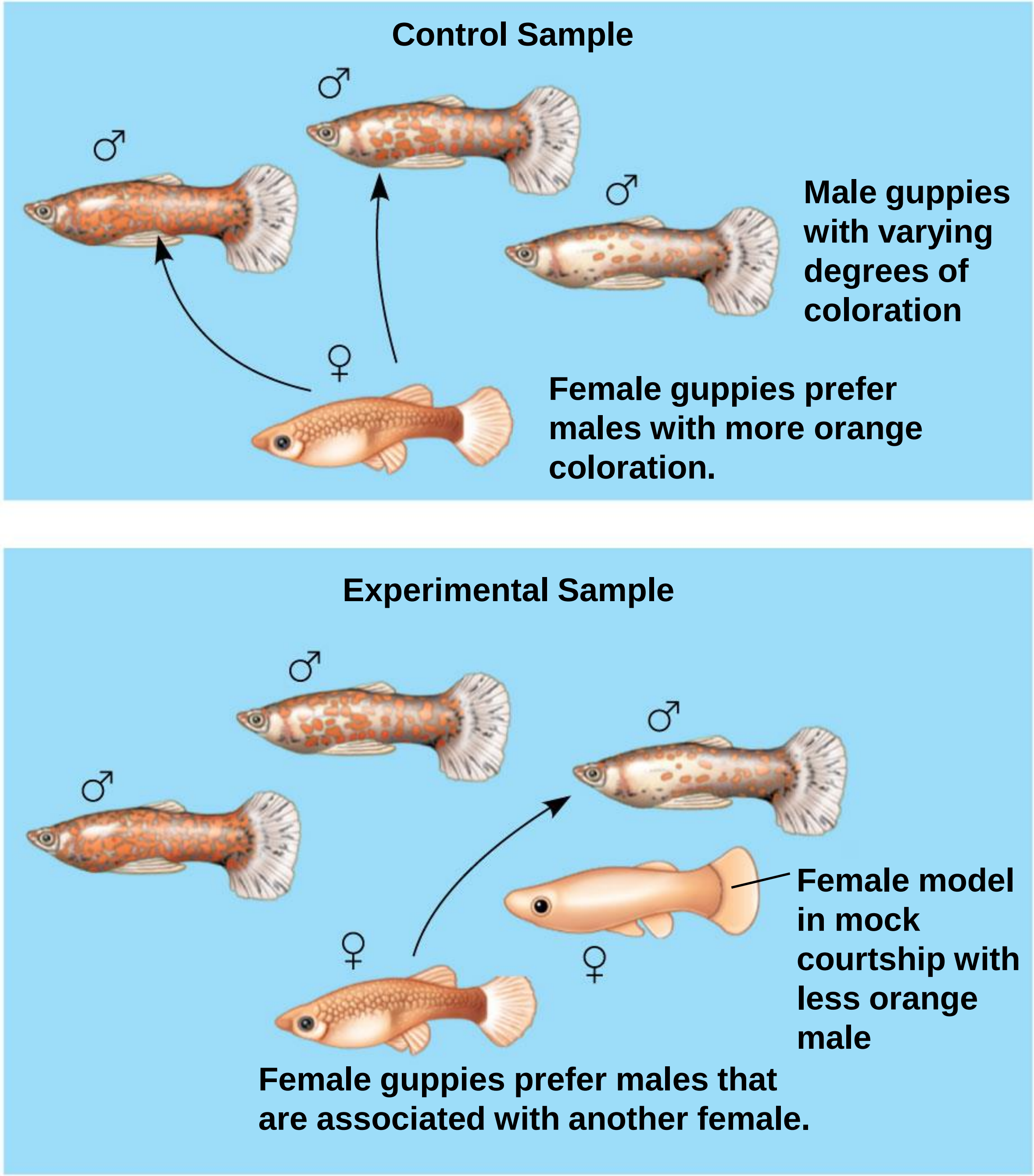
Figure 51.18

Figure 51.19


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

- **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

Figure 51.20



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 can reduce variation among males
- Such competition may involve agonistic behavior, an often ritualized contest that determines which competitor gains access to a resource

Figure 51.21

Applying Game Theory

- In some species, sexual selection has driven the evolution of alternative mating behavior and morphology in males
- The fitness of a particular phenotype (behavior or morphology) depends on the phenotypes of other individuals in the population
- **Game theory** evaluates alternative strategies where the outcome depends on each individual’s strategy and the strategy of other individuals

- For example, each side-blotched lizard has a blue, orange, or yellow throat
- Each color is associated with a specific strategy for obtaining mates
  – Orange-throat males are the most aggressive and defend large territories
  – Blue-throats defend small territories
  – Yellow-throats are nonterritorial, mimic females, and use “sneaky” strategies to mate

Figure 51.22

- 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

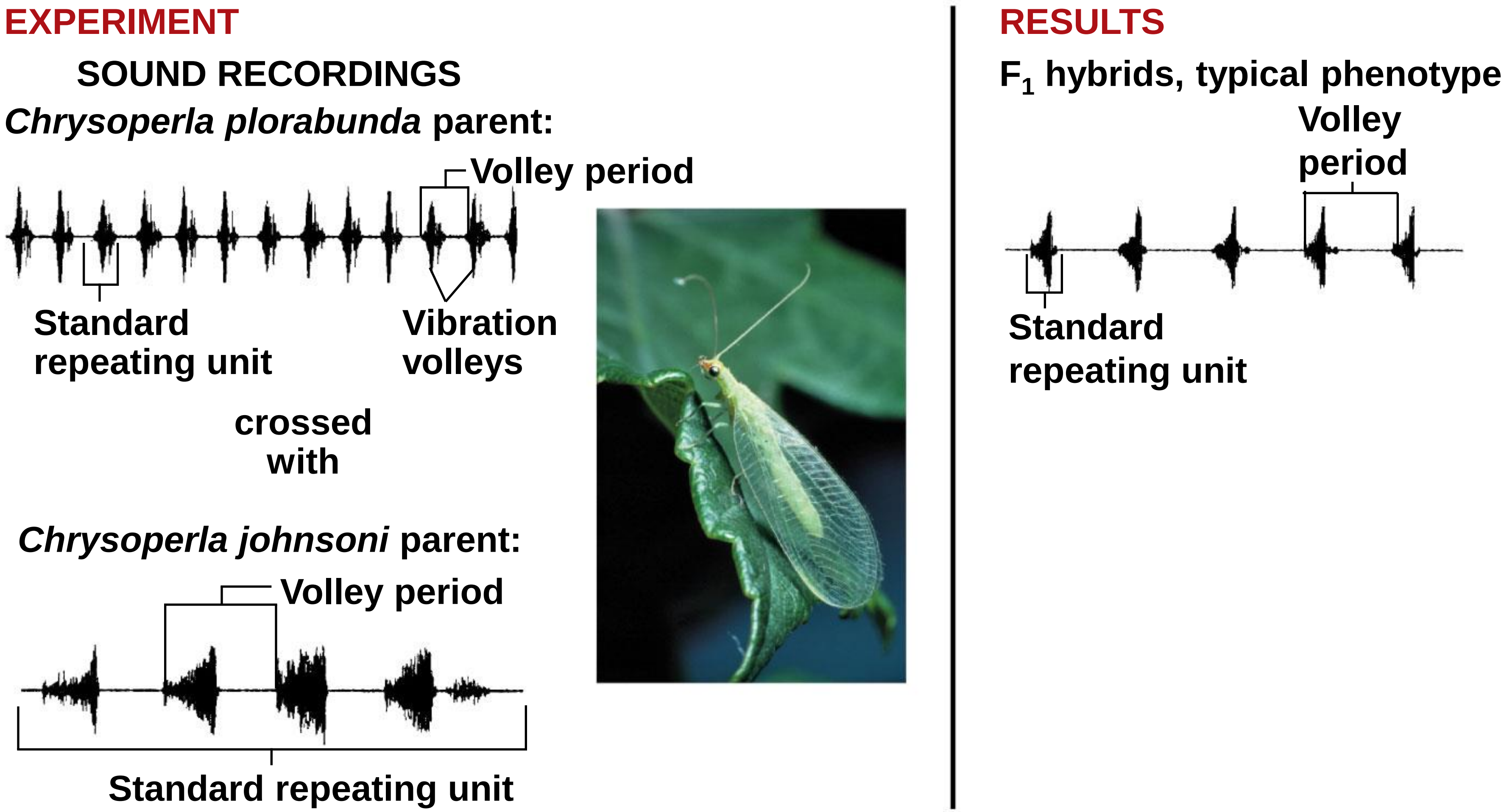
Concept 51.4: Inclusive fitness can account for the evolution of behavior, including altruism

- Animal behavior is governed by complex interactions between genetic and environmental factors
- Selfless behavior can be explained by inclusive fitness

Genetic Basis of Behavior

- A master regulatory gene can control many behaviors
  - For example, a single gene controls many behaviors of the male fruit fly courtship ritual
- Multiple independent genes can contribute to a single behavior
  - For example, in green lacewings, the courtship song is unique to each species; multiple independent genes govern different components of the courtship song

Figure 51.23


EXPERIMENT
SOUND RECORDINGS
Chrysoperla plorabunda parent:
Volley period
Standard repeating unit
Vibration volleys
crossed with
Chrysoperla johnsoni parent:
Volley period
Standard repeating unit
RESULTS
F_1 hybrids, typical phenotype:
Volley period
Standard repeating unit

- Differences at a single locus can sometimes have a large effect on behavior
  - For example, male prairie voles pair-bond with their mates, while male meadow voles do not
  - The level of a specific receptor for a neurotransmitter determines which behavioral pattern develops

Figure 51.24

Genetic Variation and the Evolution of Behavior

- When behavioral variation within a species corresponds to environmental variation, it may be evidence of past evolution

Case Study: Variation in Prey Selection

- The natural diet of western garter snakes varies by population
- Coastal populations feed mostly on banana slugs, while inland populations rarely eat banana slugs
- Studies have shown that the differences in diet are genetic
- The two populations differ in their ability to detect and respond to specific odor molecules produced by the banana slugs

Figure 51.25

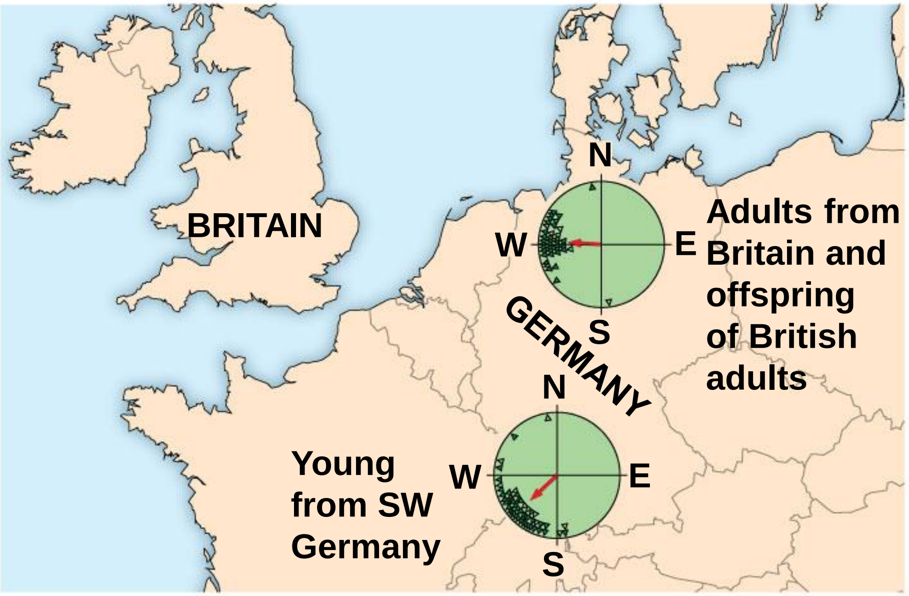
Case Study: Variation in Migratory Patterns

- Most blackcaps (birds) that breed in Germany winter in Africa, but some winter in Britain
- Under laboratory conditions, each migratory population exhibits different migratory behaviors
- The migratory behaviors are regulated by genetics

Figure 51.26

EXPERIMENT

RESULTS



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

– For example, under threat from a predator, an individual Belding’s ground squirrel will make an alarm call to warn others, even though calling increases the chances that the caller is killed
– For example, in naked mole rat populations, nonreproductive individuals may sacrifice their lives protecting their reproductive queen and kings from predators

Figure 51.27

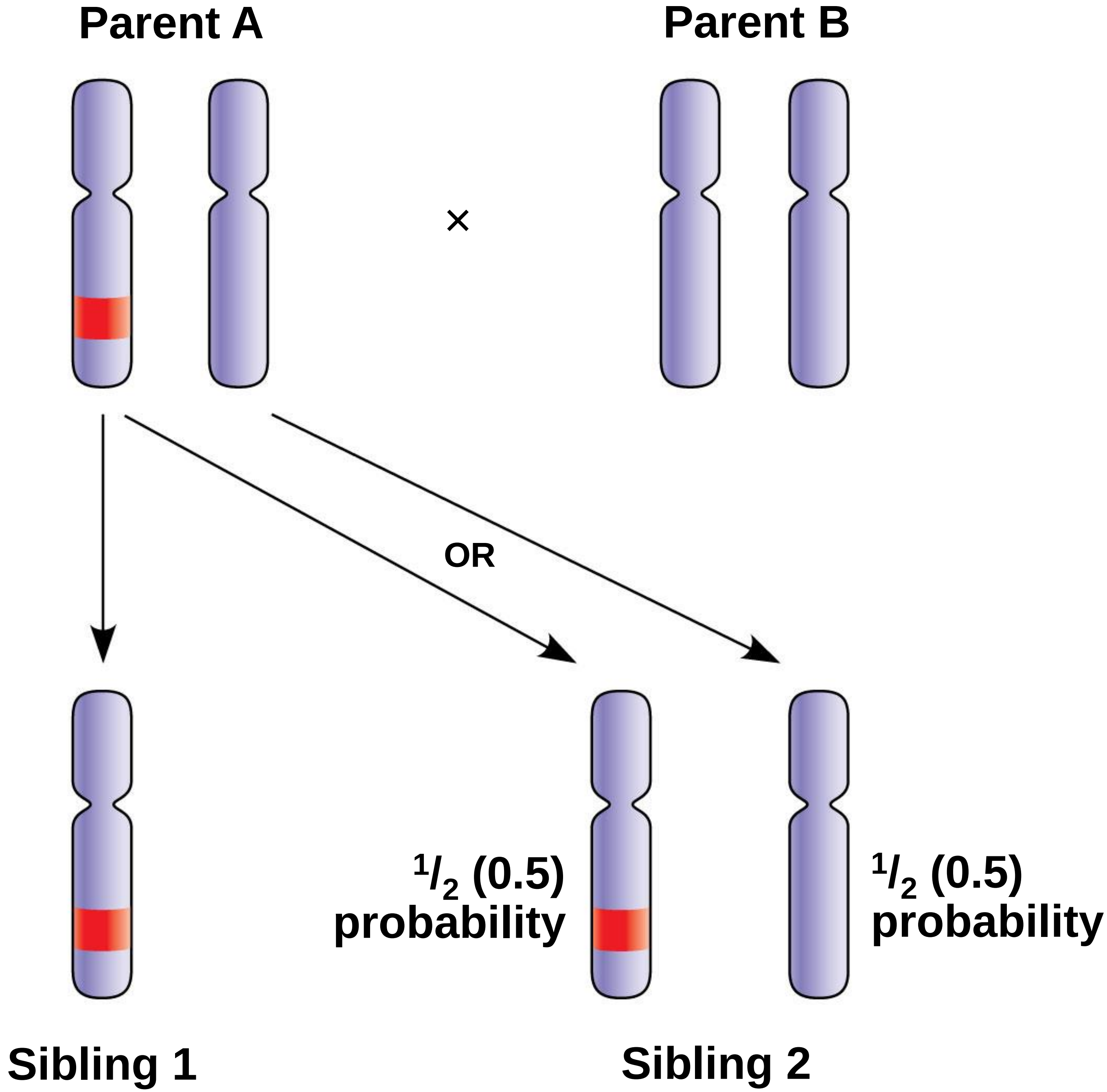
Inclusive Fitness

- 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

- 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*)

Figure 51.28



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

- Natural selection favors altruism when

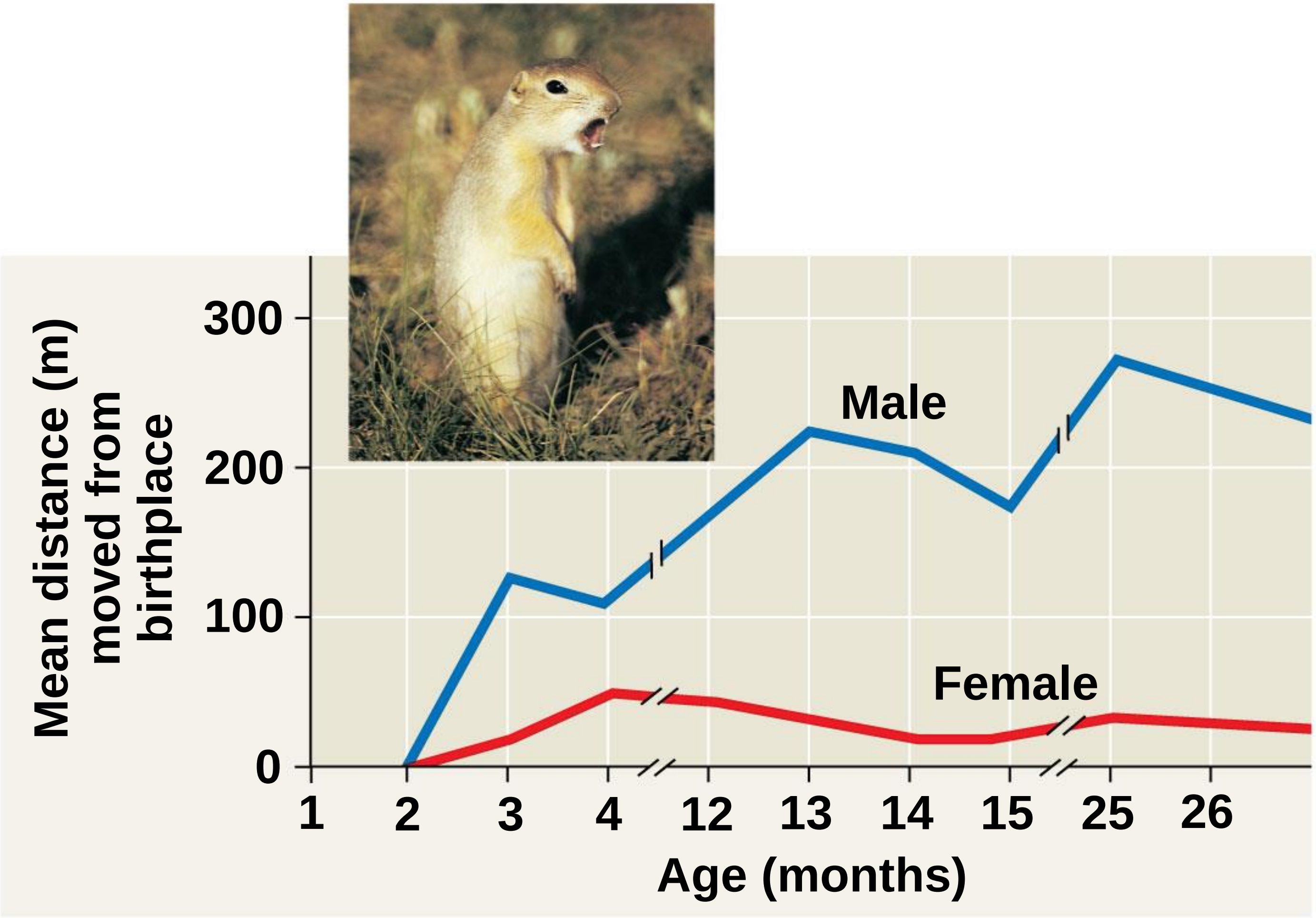
$$rB > C$$

- 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** 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
- 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

Figure 51.29


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

- Naked mole rats living within a colony are closely related
- Nonreproductive individuals increase their inclusive fitness by helping the reproductive queen and kings (their close relatives) to pass their genes to the next generation

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**

- Reciprocal altruism is limited to species with stable social groups where individuals meet repeatedly, and cheaters (who don’t reciprocate) are punished
- Reciprocal altruism has been used to explain altruism between unrelated individuals in humans

- In game theory, a tit-for-tat strategy has 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

- Tit-for-tat strategy explains how reciprocal altruism could have evolved
- Individuals who engage in a tit-for-tat strategy have a higher fitness than individuals who are always selfish

Evolution and Human Culture

- No other species comes close to matching the social learning and cultural transmission that occur among humans
- Human culture is related to evolutionary theory in the distinct discipline of **sociobiology**
- Human behavior, like that of other species, results from interaction 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

Figure 51.UN01

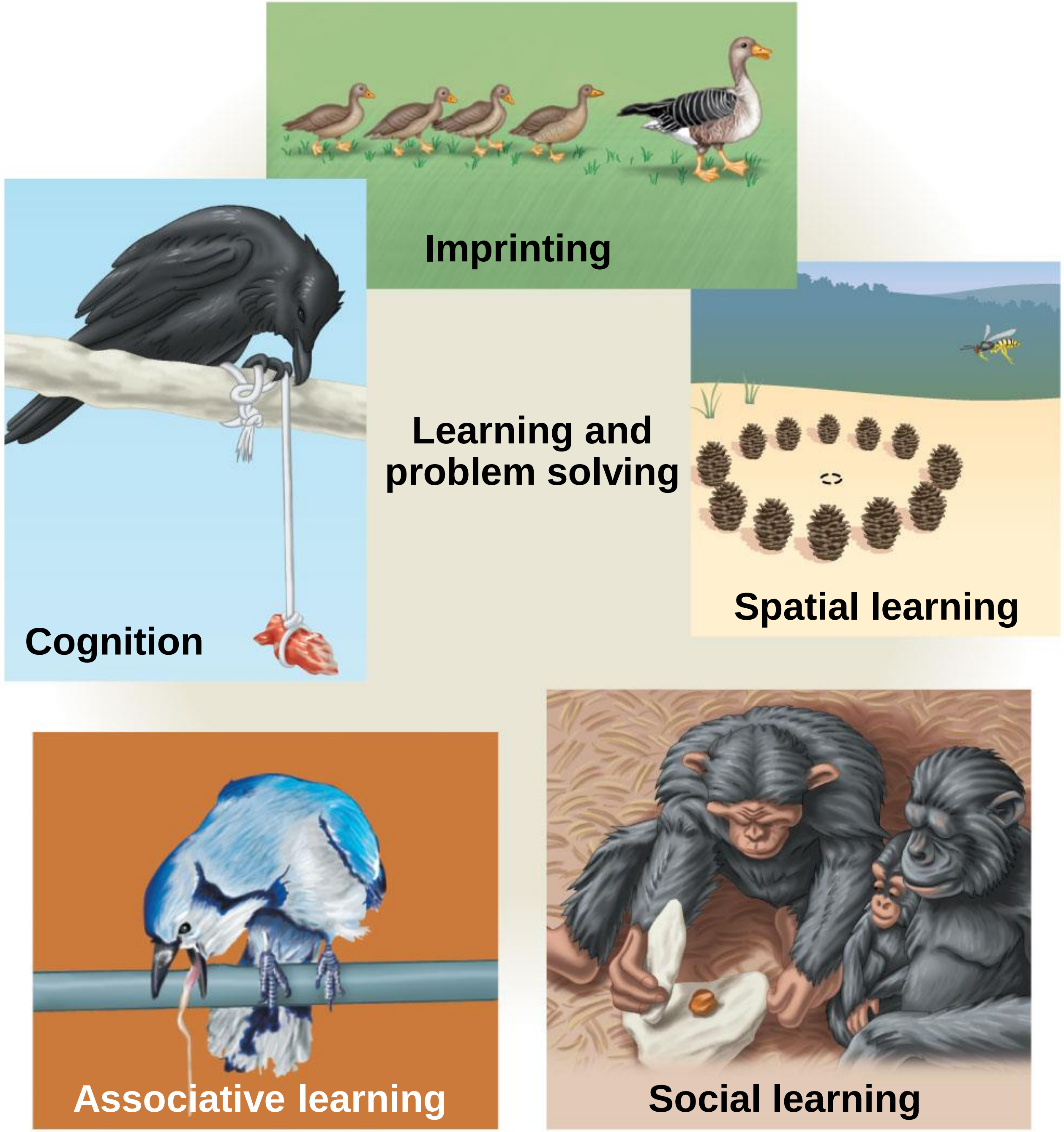


Figure 51.UN02