Chapter 51

Animal Behavior

PowerPoint® Lecture Presentations for

Biology

Eighth Edition

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Overview: Shall We Dance?

- Cranes engage in interesting dancing behavior during courtship
- Animal behavior is based on physiological systems and processes
- A **behavior** is the nervous system's response to a stimulus and is carried out by the muscular or the hormonal system

Fig. 51-1

- Behavior helps an animal
  - Obtain food
  - Find a partner for sexual reproduction
  - Maintain homeostasis
- Behavior is subject to natural selection

PLAY Video: Albatross Courtship Ritual

PLAY Video: Blue-footed Boobies Courtship Ritual

PLAY Video: Giraffe Courtship Ritual

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

- An animal's behavior is its response to external and internal stimuli

Fig. 51-2

- **Ethology** is the scientific study of animal behavior, particularly in natural environments

- According to early ethologist Niko Tinbergen, four questions should be asked about 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 mechanisms?

3. How does the behavior aid survival and reproduction?

4. What is the behavior's evolutionary history?

- These questions highlight the complementary nature of proximate and ultimate perspectives

- **Proximate causation**, or “how” explanations, focus on
  - Environmental stimuli that trigger a behavior
  - Genetic, physiological, and anatomical mechanisms underlying a behavior
- **Ultimate causation**, or “why” explanations, focus on
  - Evolutionary significance of a behavior

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

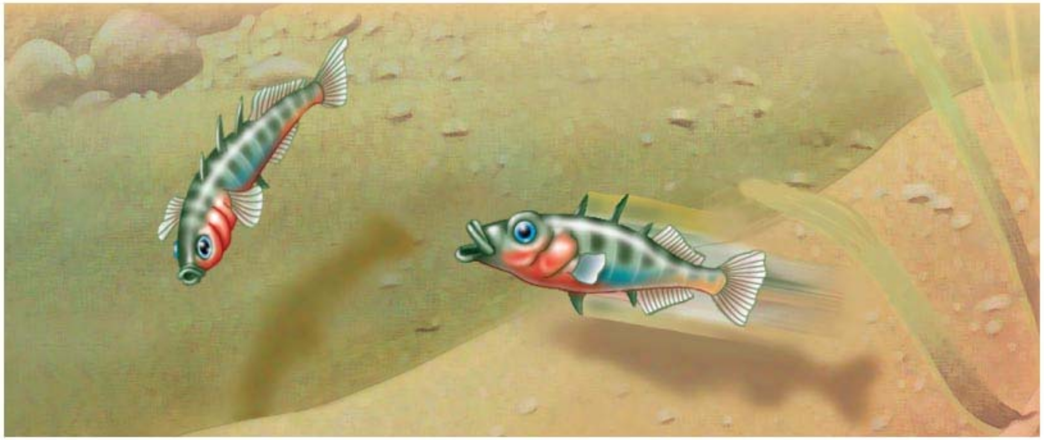
- It integrates proximate and ultimate explanations for animal behavior

Fixed Action Patterns

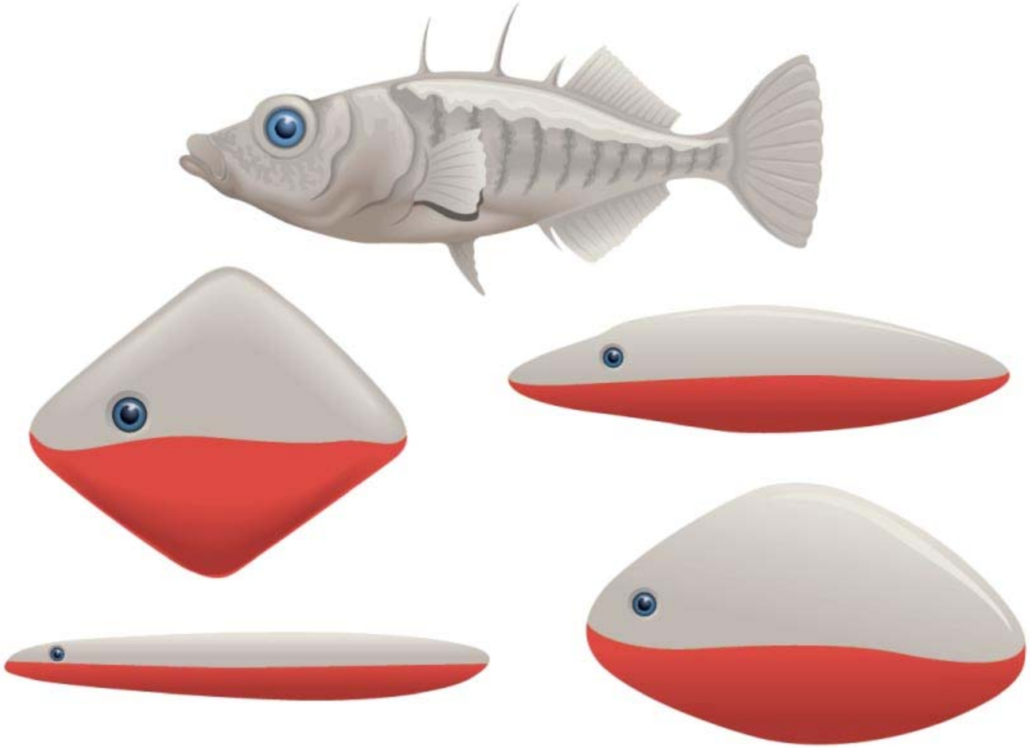
- A **fixed action pattern** is a sequence of unlearned, innate behaviors that is unchangeable
- Once initiated, it is usually carried to completion
- A fixed action pattern is triggered by an external cue known as a **sign stimulus**

- 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

Fig. 51-3



(a)



(b)

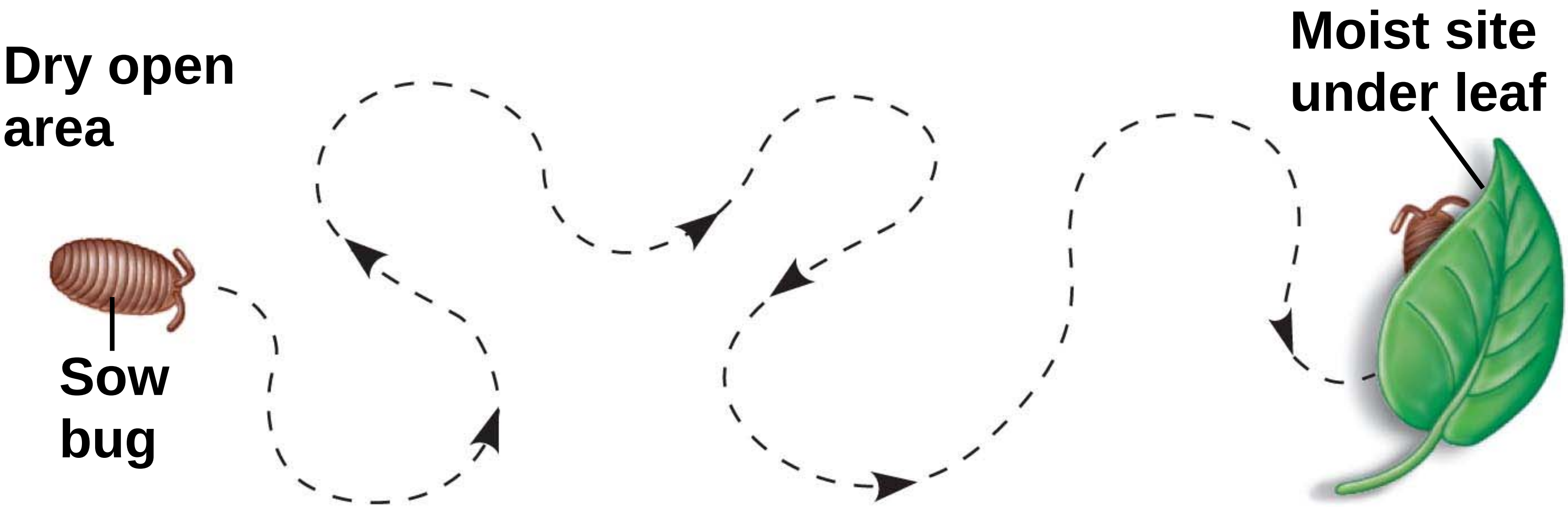
Oriented Movement

- Environmental cues can trigger movement in a particular direction

Kinesis and Taxis

- 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
- Though sow bug behavior varies with humidity, sow bugs do not move toward or away from specific moisture levels

Fig. 51-4



- A **taxis** is a more or less automatic, oriented movement toward or away from a stimulus
- Many stream fish exhibit a positive taxis and 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

Migration

- **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

Fig. 51-5

Behavioral Rhythms

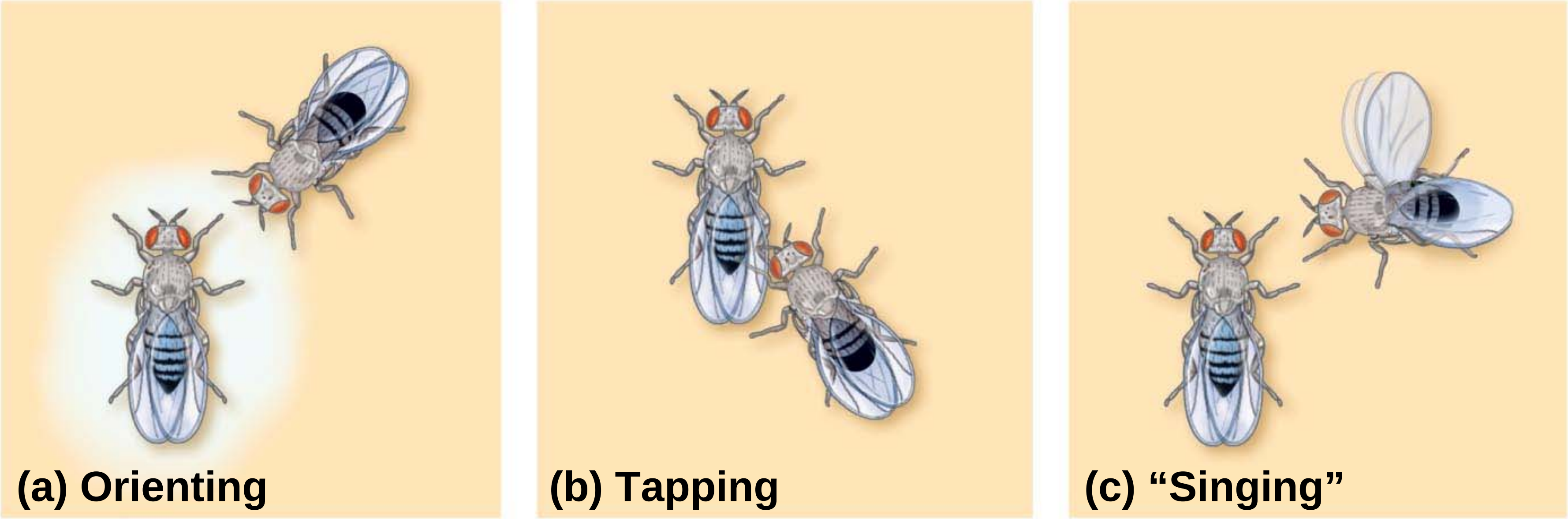
- Some animal behavior is affected by the animal's circadian rhythm, a daily cycle of rest and activity
- Behaviors such as migration and reproduction are linked to changing seasons, or a *circannual rhythm*
- Some behaviors are linked to lunar cycles
  - For example, courtship in fiddler crabs occurs during the new and full moon

Fig. 51-6

Animal Signals and Communication

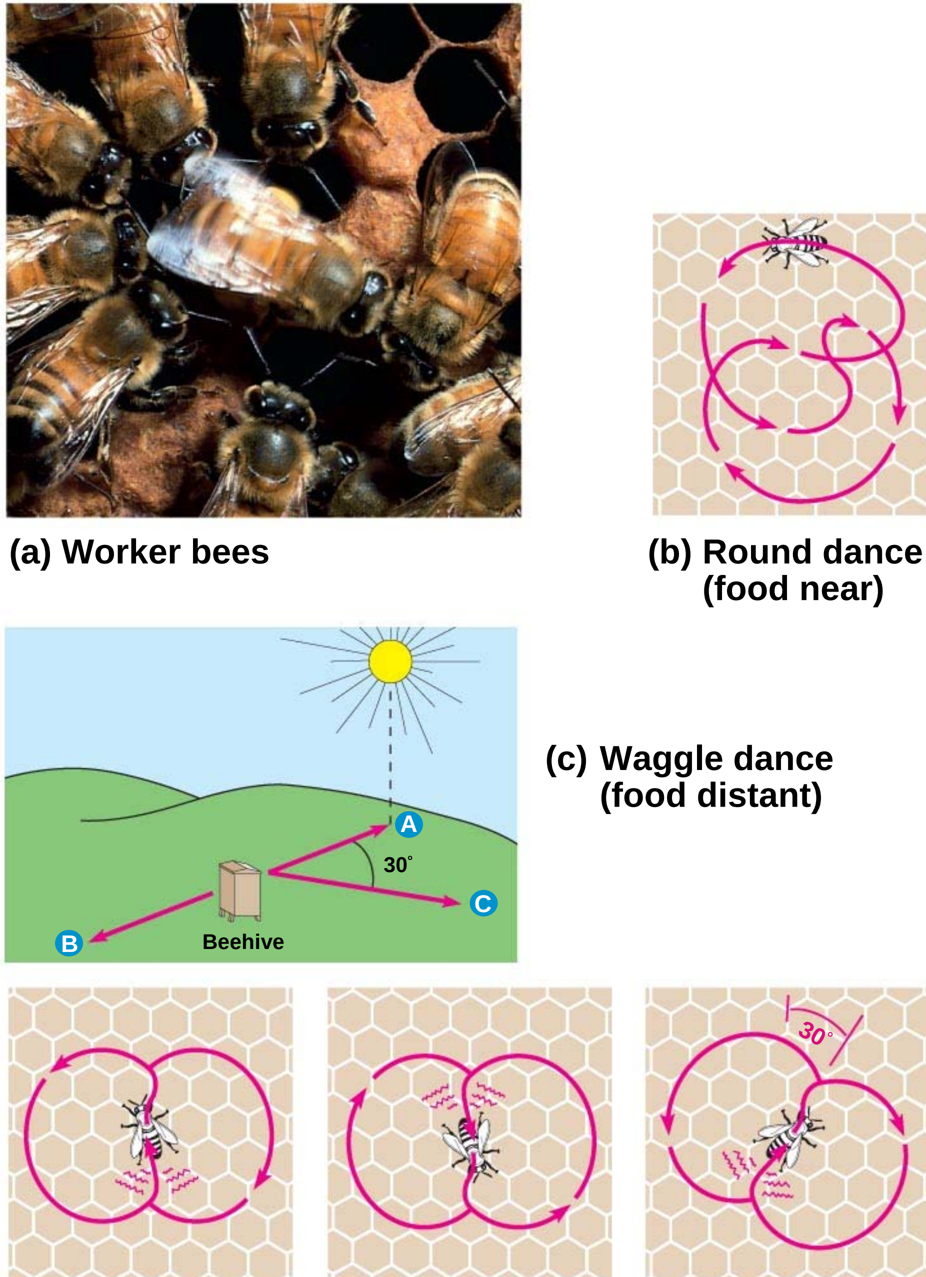
- In behavioral ecology, a **signal** is a behavior that causes a change in another animal's behavior
- **Communication** is the transmission and reception of signals
- Animals communicate using visual, chemical, tactile, and auditory signals
- The type of signal is closely related to lifestyle and environment

Fig. 51-7



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

Fig. 51-8



(a) Worker bees

(b) Round dance (food near)

(c) Waggle dance (food distant)

Location A

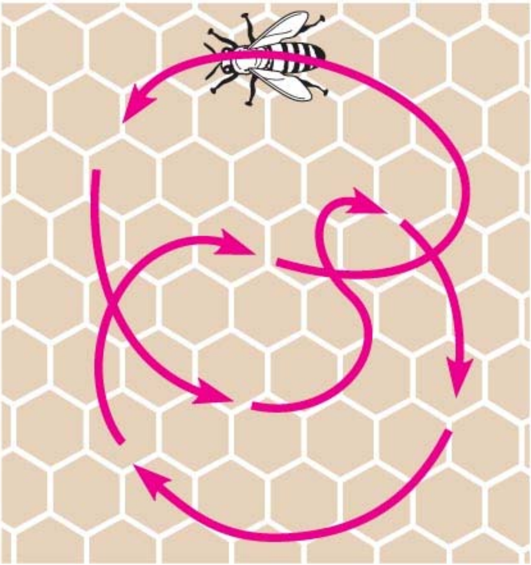
Location B

Location C

Fig. 51-8a

(a) Worker bees

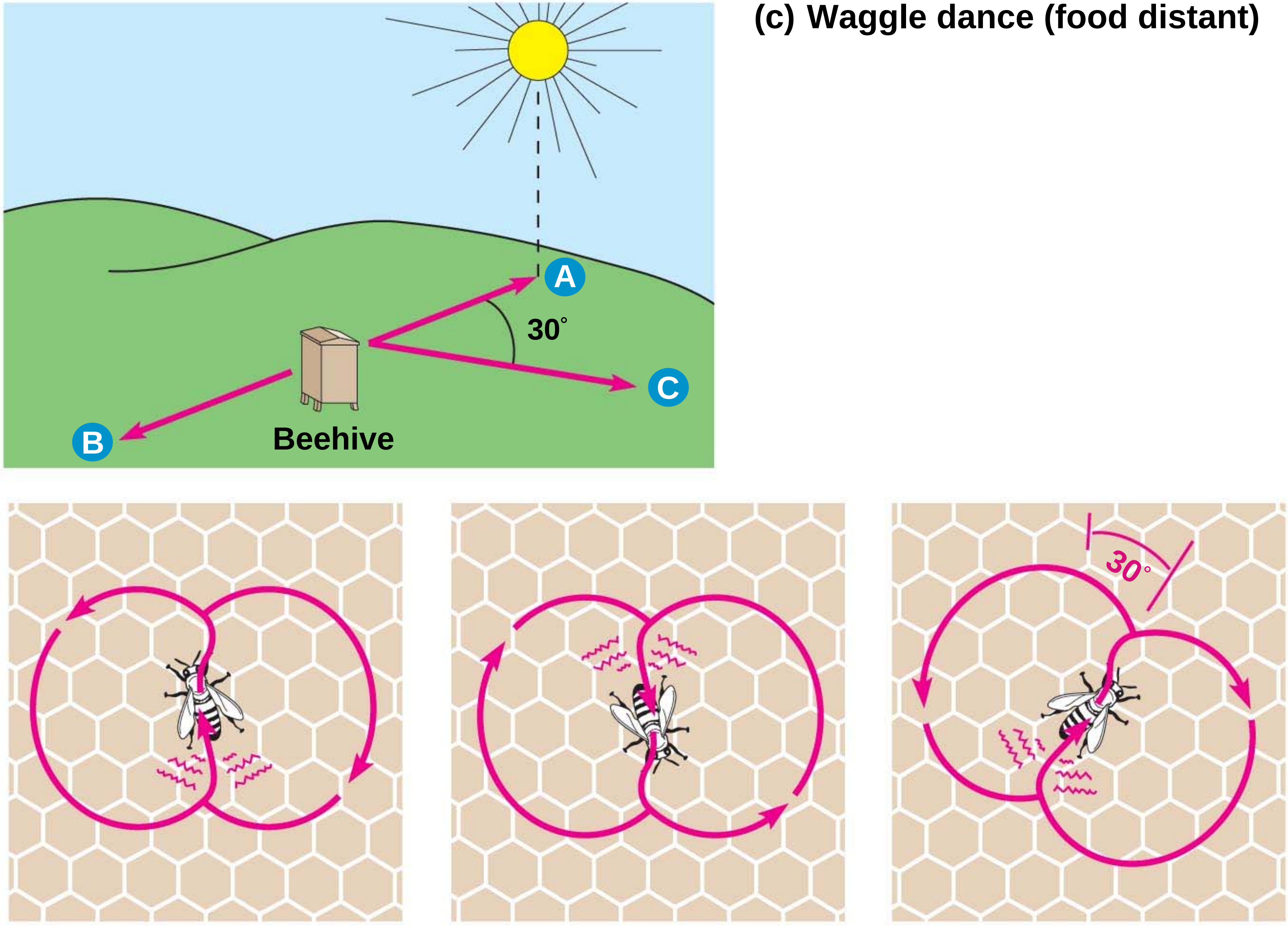
Fig. 51-8b



(b) Round dance (food near)

Fig. 51-8c

(c) Waggle dance (food distant)



Location A

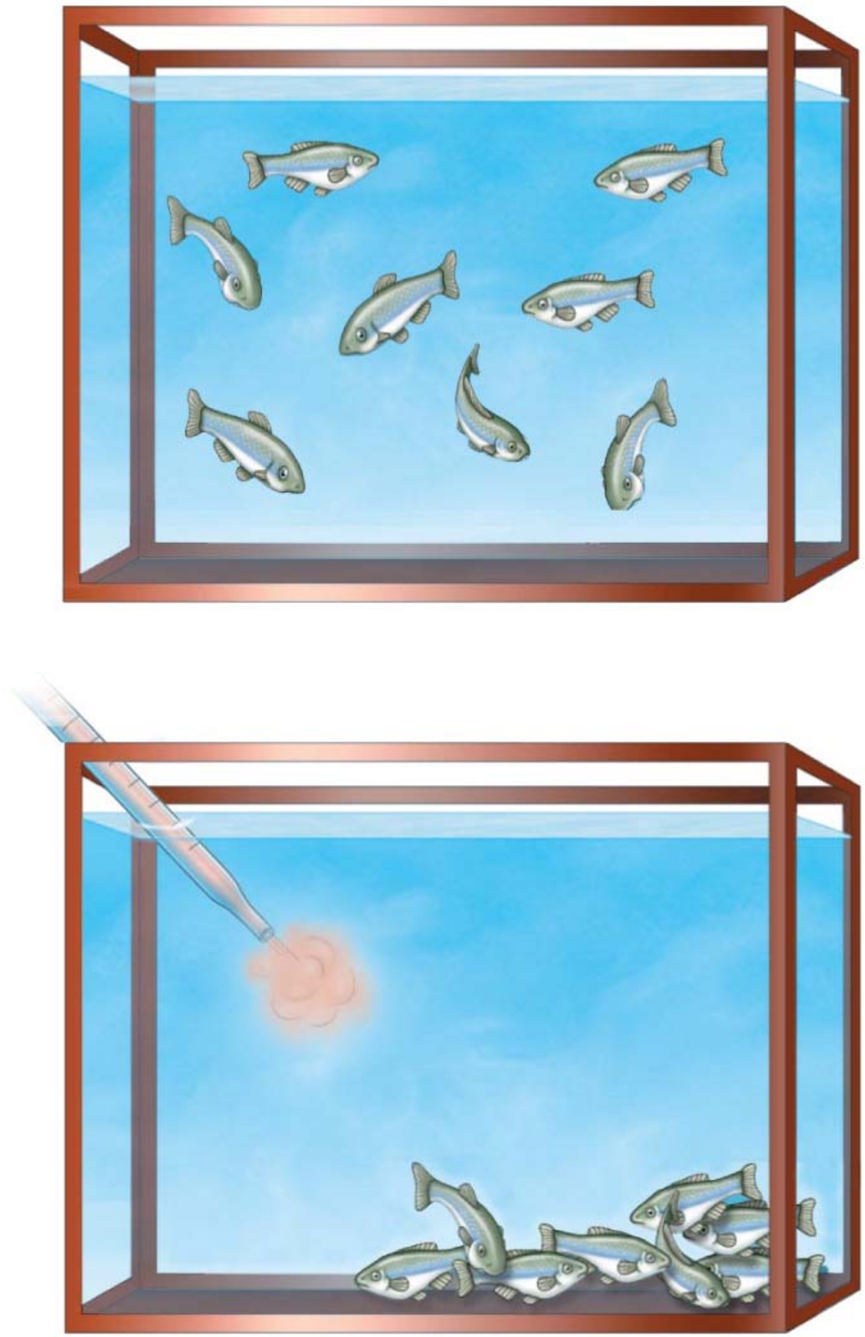
Location B

Location C

Pheromones

- Many animals that communicate through odors emit chemical substances called **pheromones**
- Pheromones are effective at very low concentrations
- 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

Fig. 51-9



(a) Minnows before alarm

(b) Minnows after alarm

Concept 51.2: Learning establishes specific links between experience and behavior

- **Innate behavior** is developmentally fixed and under strong genetic influence
- **Learning** is the modification of behavior based on specific experiences

Habituation

- **Habituation** is a simple form of learning that involves loss of responsiveness to stimuli that convey little or no information
  - For example, birds will stop responding to alarm calls from their species if these are not followed by an actual attack

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

PLAY

Video: Ducklings

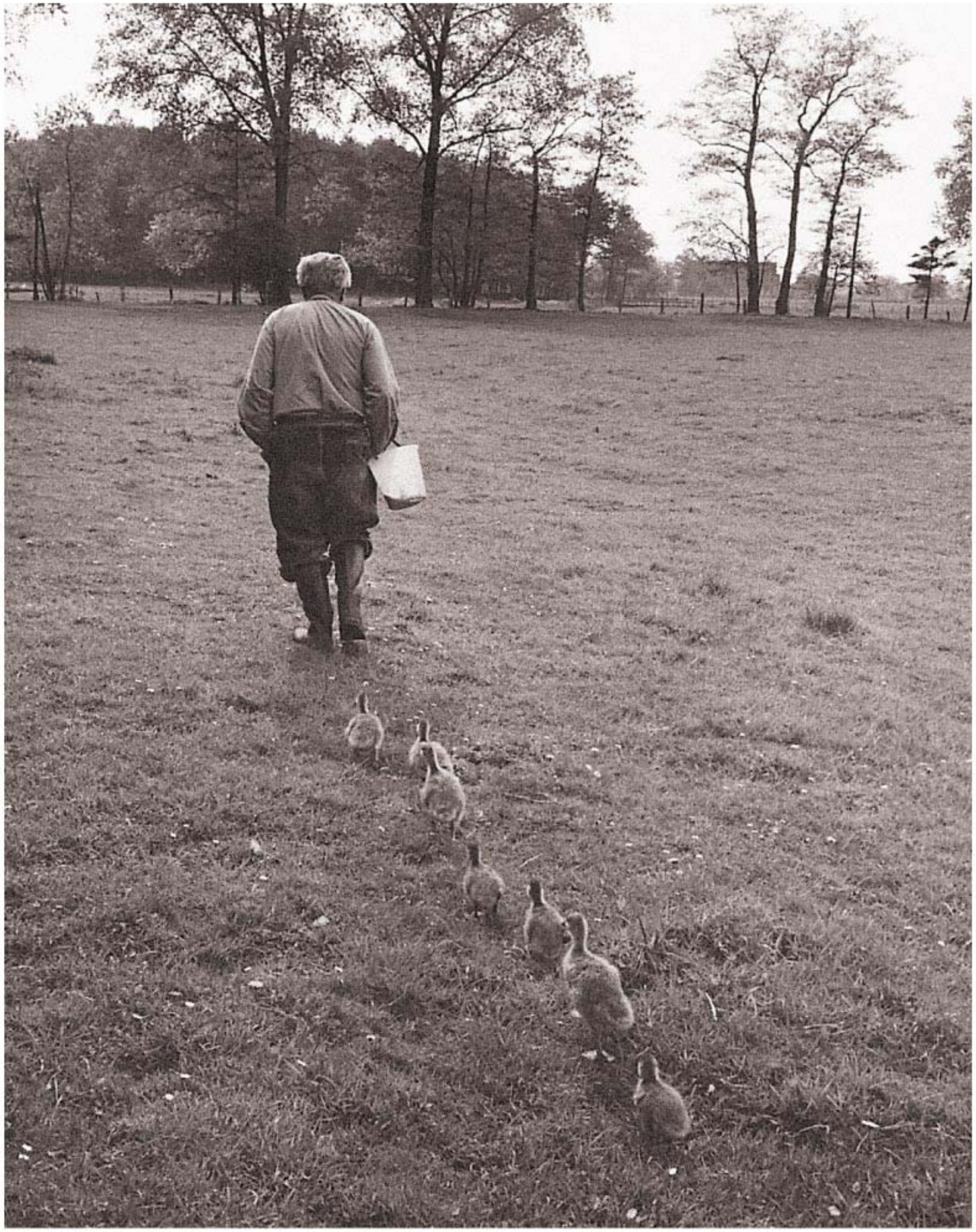
- Conservation biologists have taken advantage of imprinting in programs to save the whooping crane from extinction
- Young whooping cranes can imprint on humans in “crane suits” who then lead crane migrations using ultralight aircraft

Fig. 51-10

(a) Konrad Lorenz and geese

(b) Pilot and cranes

Fig. 51-10a



(a) Konrad Lorenz and geese

Fig. 51-10b

(b) Pilot and cranes

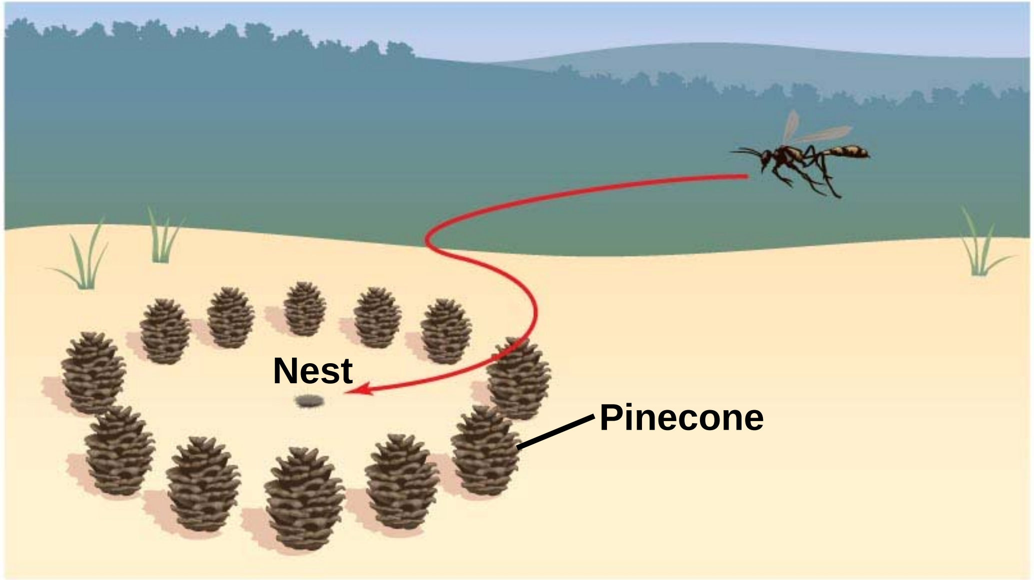
Spatial Learning

- **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

PLAY Video: Bee Pollinating

Fig. 51-11

EXPERIMENT



RESULTS

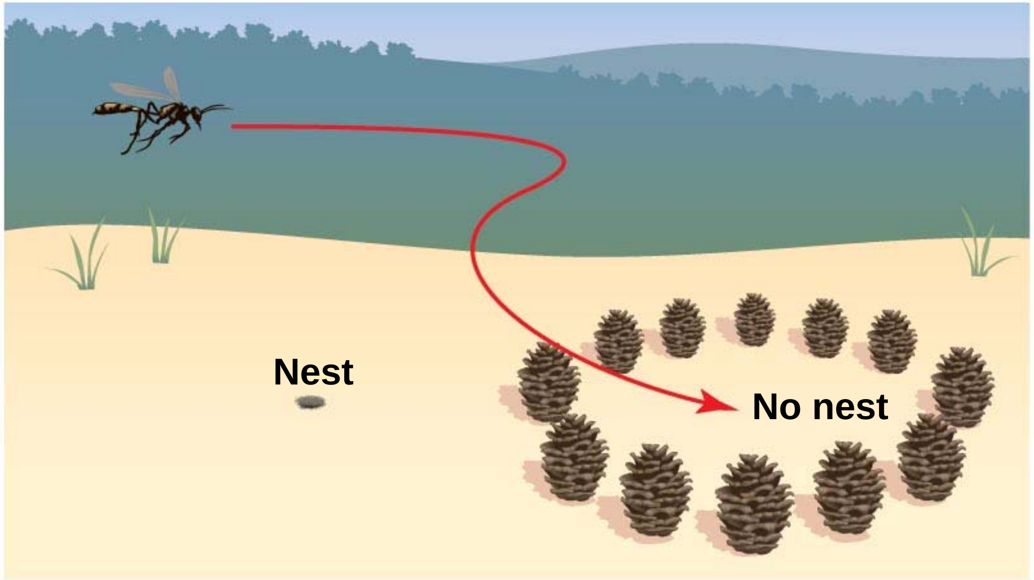


Fig. 51-11a

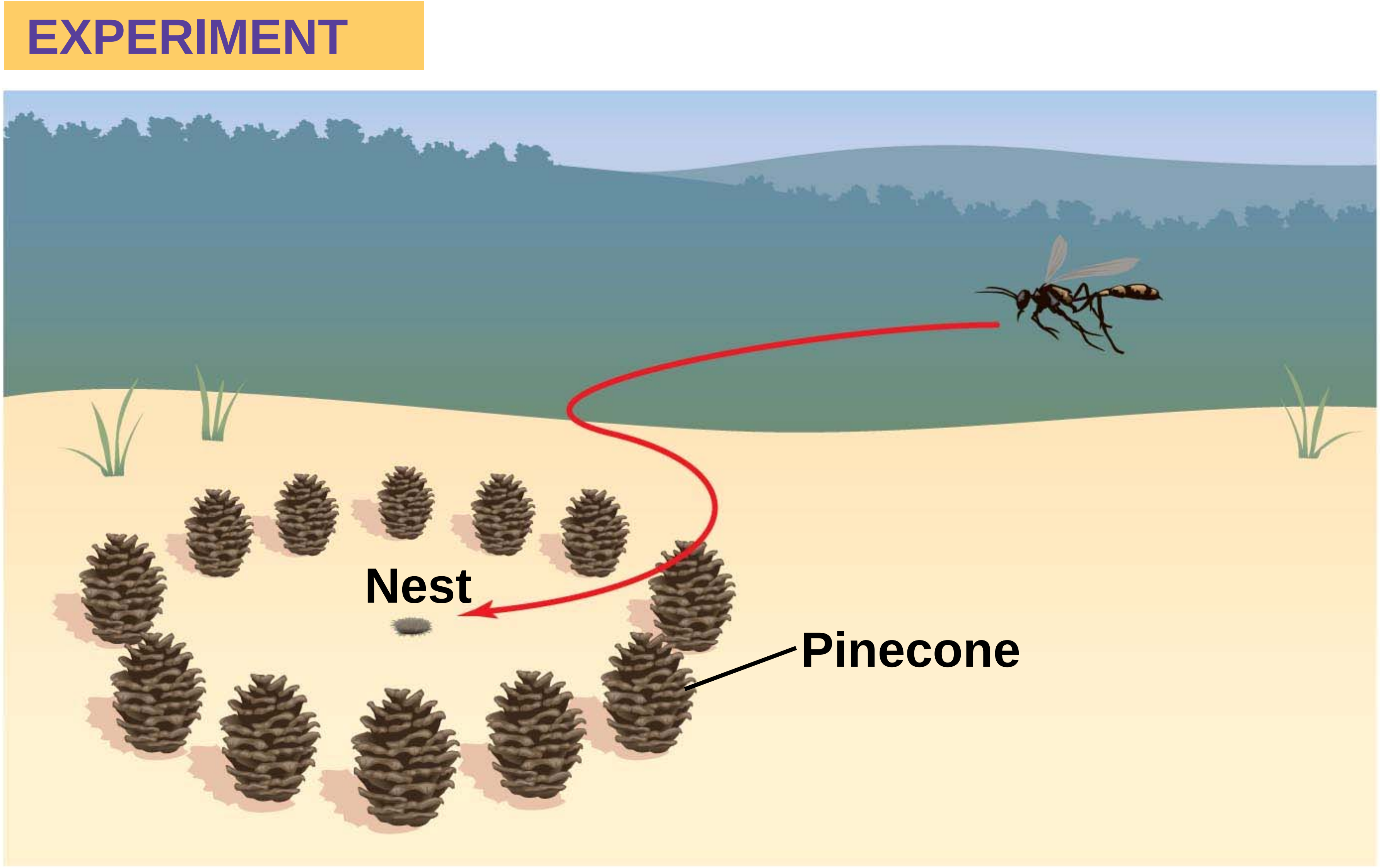
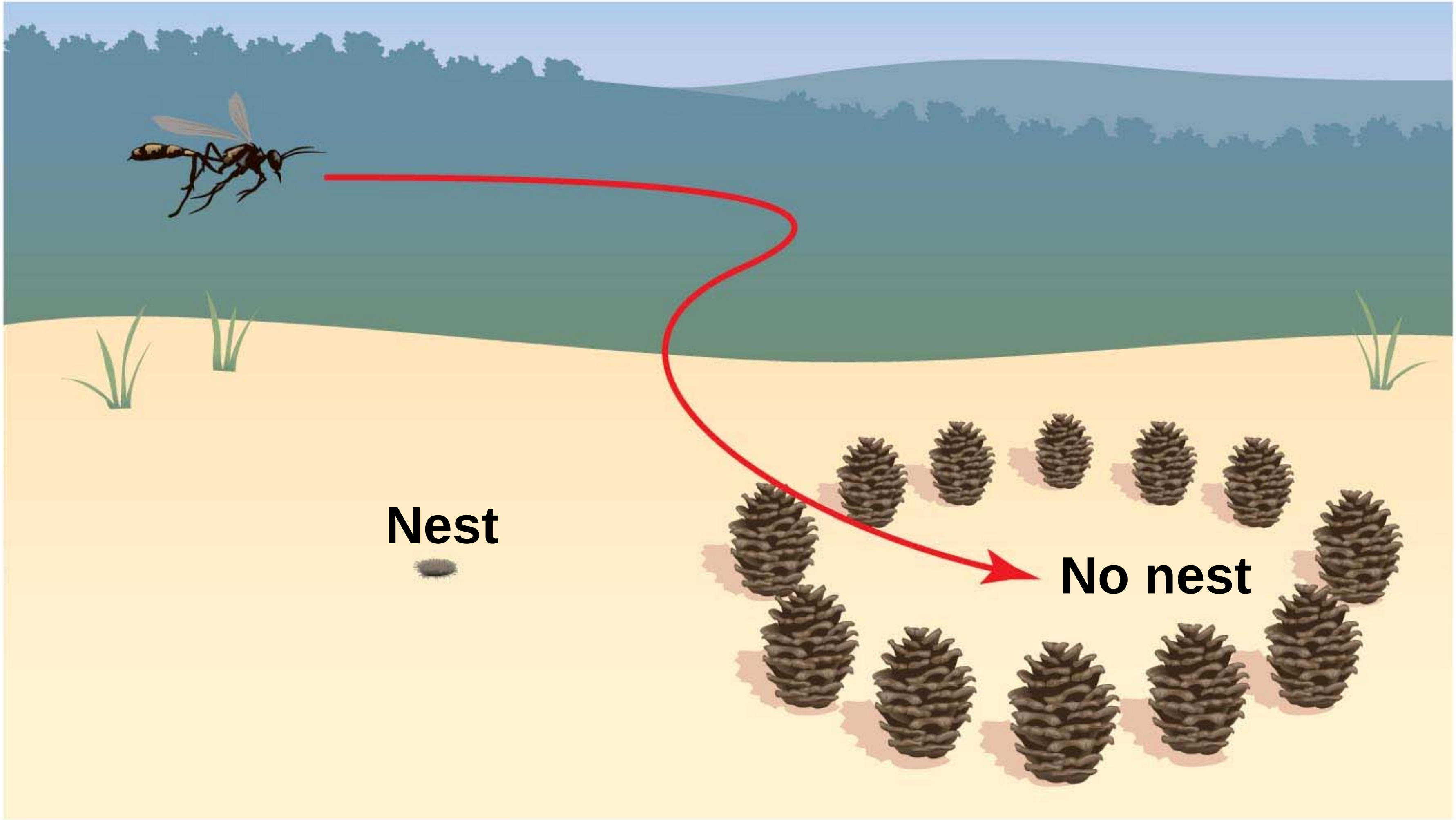


Fig. 51-11b

RESULTS



Cognitive Maps

- 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

Fig. 51-12

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”

- **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
- Some animals learn to solve problems by observing other individuals
  - For example, young chimpanzees learn to crack palm nuts with stones by copying older chimpanzees

PLAY Video: Chimp Cracking Nut

Fig. 51-13

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

Concept 51.3: Both genetic makeup and environment contribute to the development of behaviors

- Animal behavior is governed by complex interactions between genetic and environmental factors

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

Regulatory Genes and Behavior

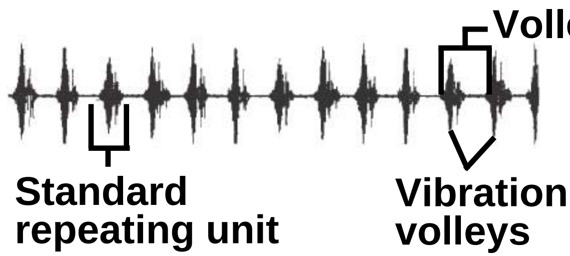
- A master regulatory gene can control many behaviors
  - For example, a single gene controls many behaviors of the male fruit fly courtship ritual
- Multiple independent genes can contribute to a single behavior
  - For example, in green lacewings, the courtship song is unique to each species; multiple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

Fig. 51-14

EXPERIMENT

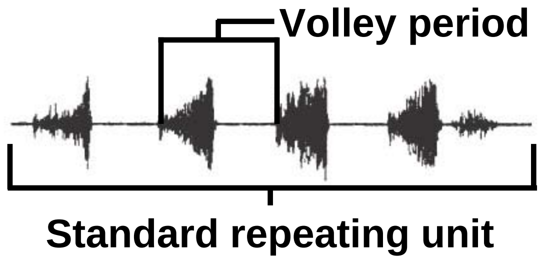
SOUND RECORDINGS

***Chrysoperla plorabunda* parent:**



crossed with

***Chrysoperla johnsoni* parent:**



RESULTS

F_1 hybrids, typical phenotype:

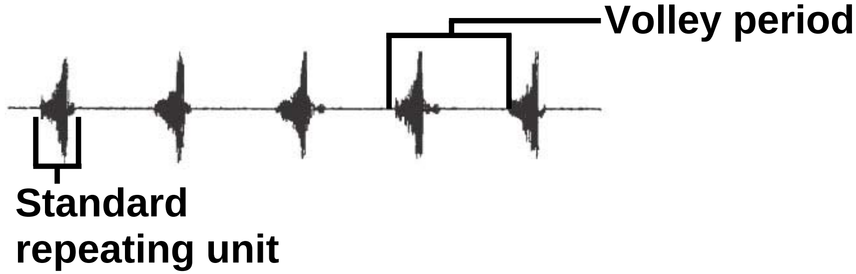


Fig. 51-14a

EXPERIMENT

SOUND RECORDINGS

Chrysoperla plorabunda **parent:**

crossed with

Chrysoperla johnsoni **parent:**

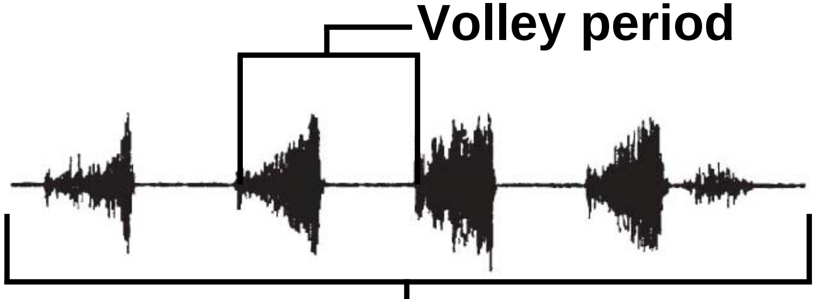
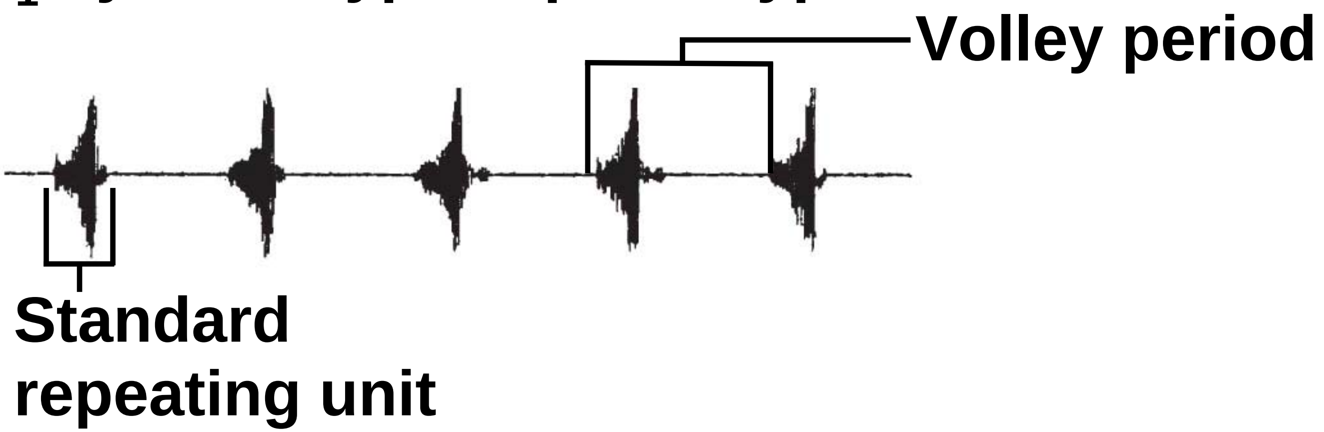


Fig. 51-14b

RESULTS

F_1 hybrids, typical phenotype:



Genetically Based Behavioral Variation in Natural Populations

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

Case Study: *Variation in Migratory Patterns*

- Most blackcaps (birds) that breed in Germany winter in Africa, but some winter in Britain
- The two migratory populations are genetically distinct

Fig. 51-15

EXPERIMENT

RESULTS

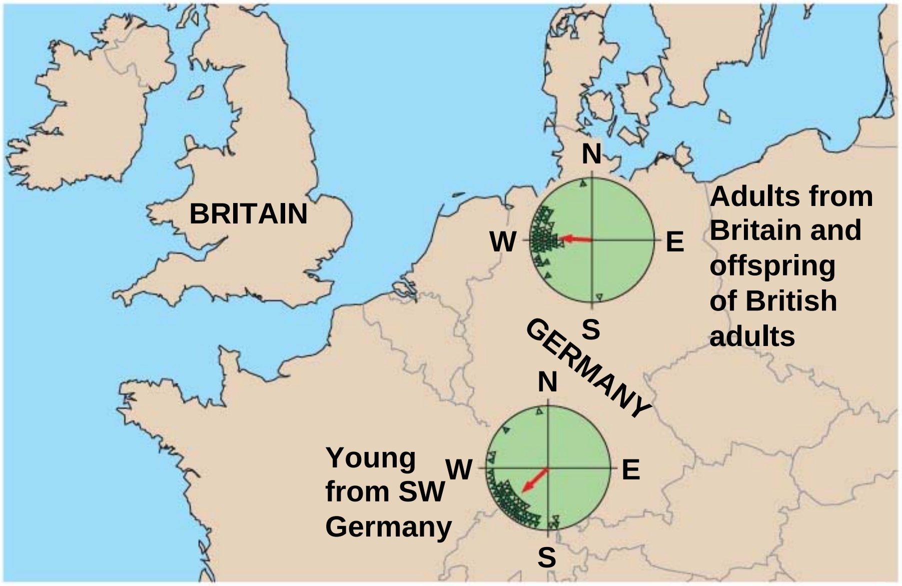


Fig. 51-15a

EXPERIMENT

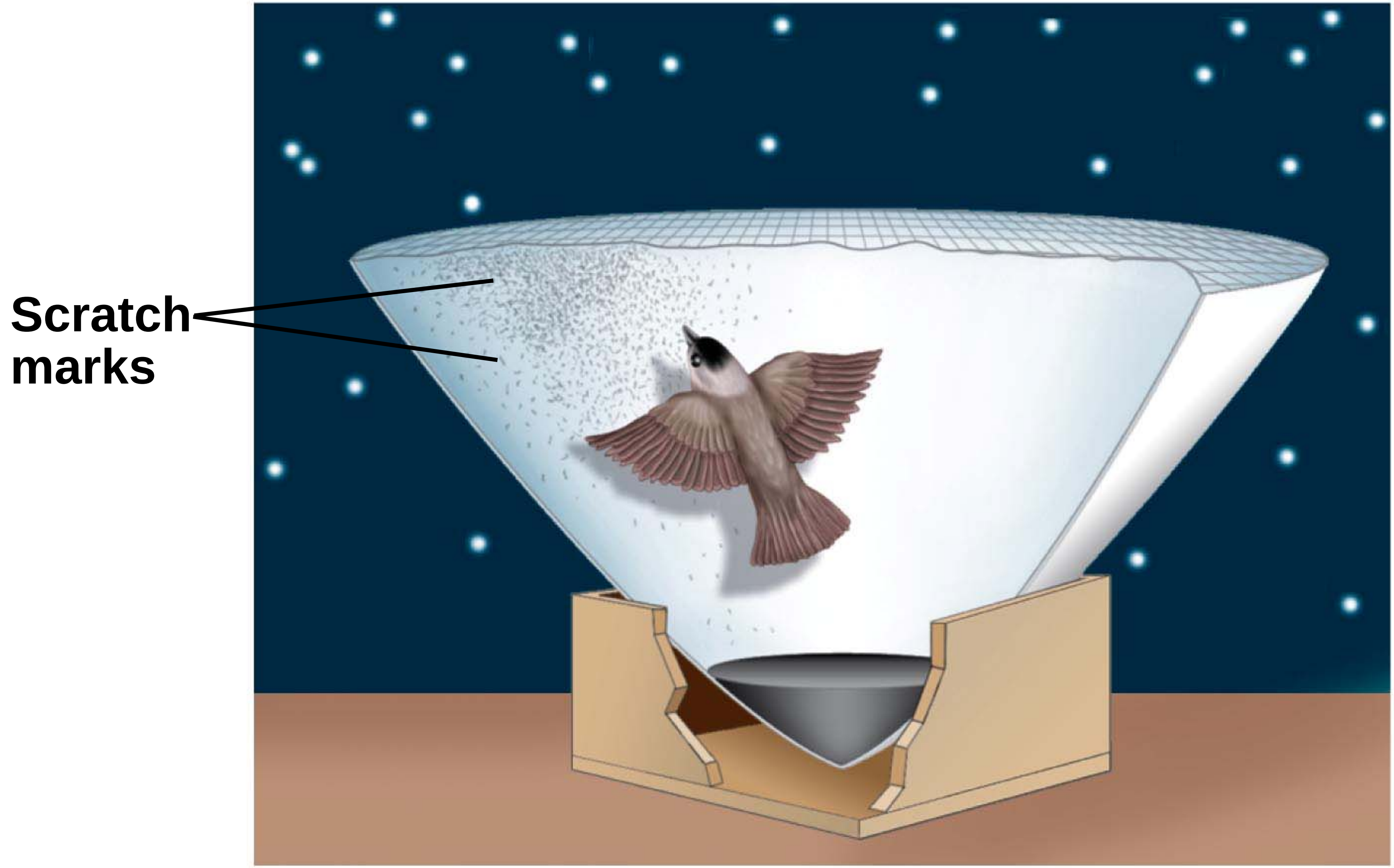
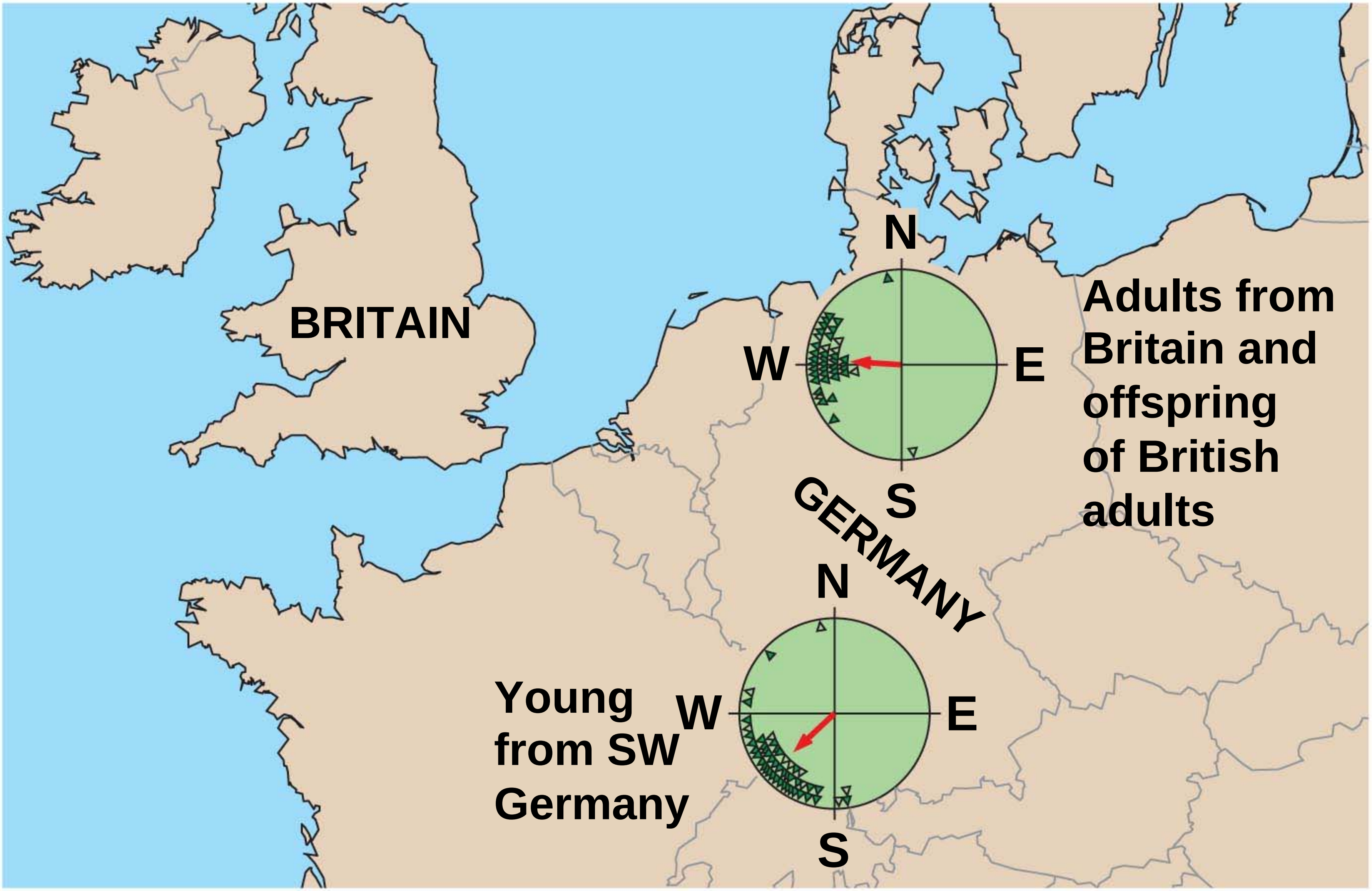


Fig. 51-15b

RESULTS



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

Fig. 51-16

Influence of Single-Locus Variation

- 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

Fig. 51-17

Concept 51.4: Selection for individual survival and reproductive success can explain most behaviors

- Genetic components of behavior evolve through natural selection
- Behavior can affect fitness by influencing foraging and mate choice

Foraging Behavior

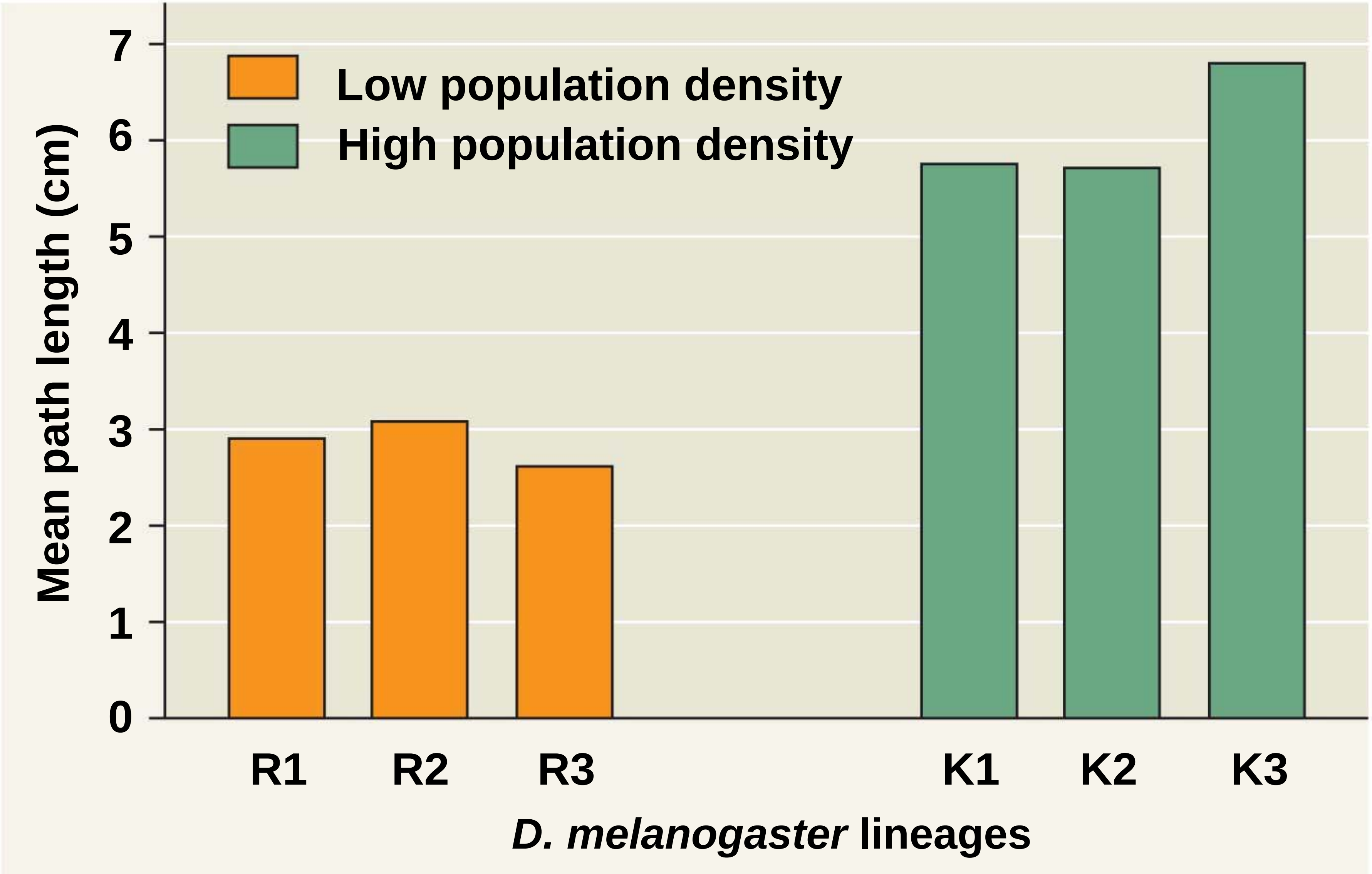
- Natural selection refines behaviors that enhance the efficiency of feeding
- **Foraging**, or food-obtaining behavior, includes recognizing, searching for, capturing, and eating food items

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 foraging behavior depending on the density of the population

Fig. 51-18



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

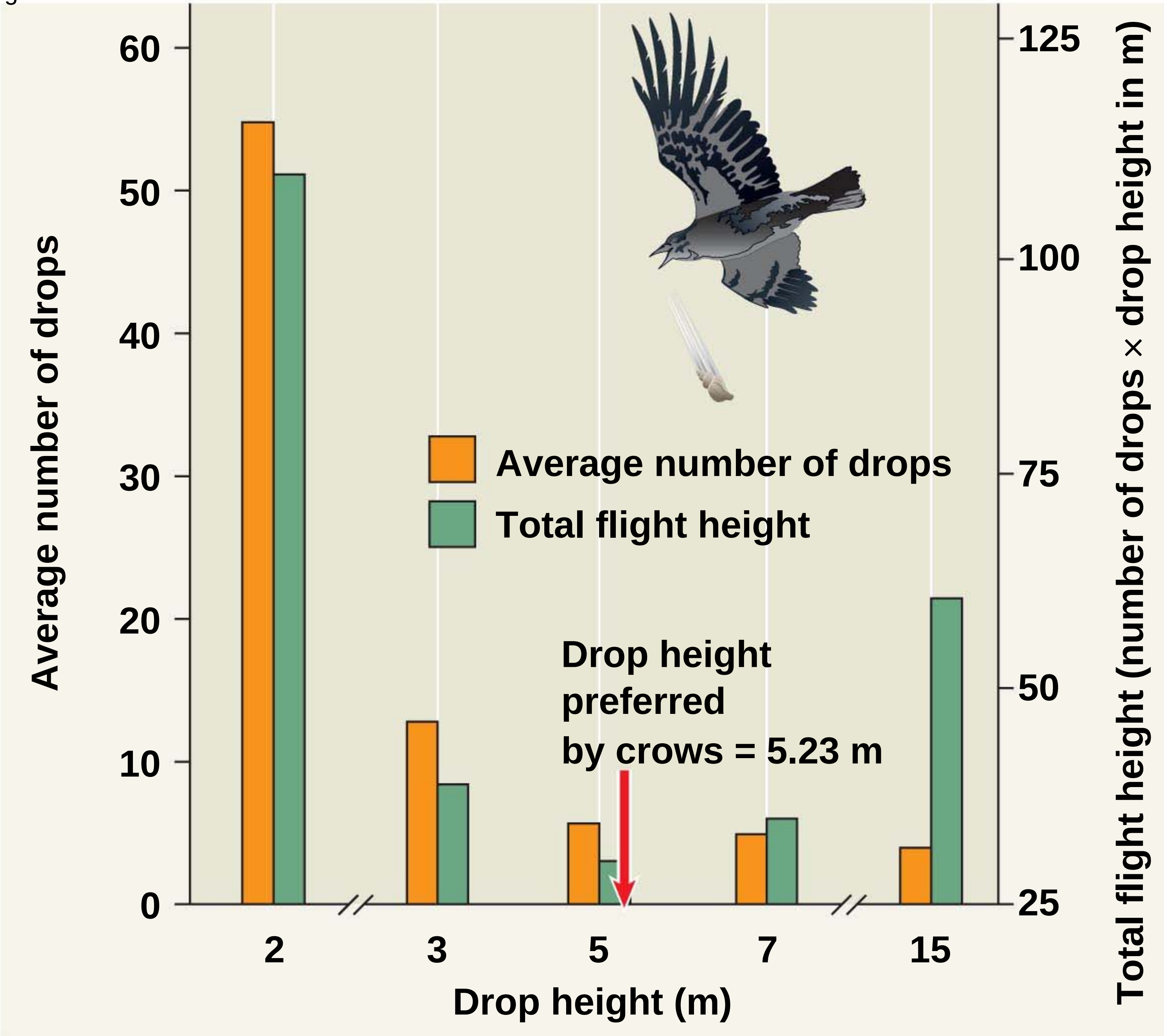
Optimal Foraging Model

- **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 5.2 m

Fig. 51-19



Average number of drops
60
50
40
30
20
10
0
Total flight height (number of drops × drop height in m)
125
100
75
50
25
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, and competing for mates
- Mating behavior results from a type of natural selection called sexual selection

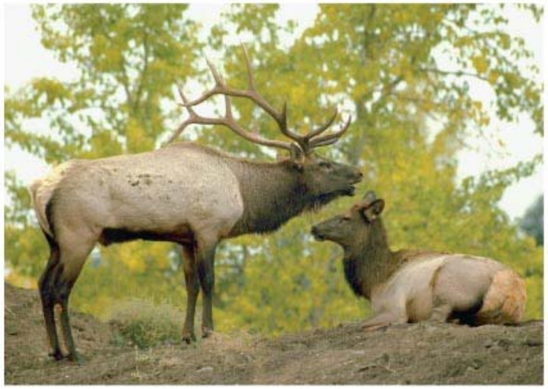
Mating Systems and Parental Care

- 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

Fig. 51-20

(a) Monogamous species



(b) Polygynous species

(c) Polyandrous species

Fig. 51-20a

(a) Monogamous 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

Fig. 51-20b

(b) Polygynous species

- In **polyandry**, one female mates with many males
- The females are often more showy than the males
- Polyandry is a rare mating system

Fig. 51-20c

(c) Polyandrous species

- 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)
- Females can be certain that eggs laid or young born contain her genes; however, paternal certainty depends on mating behavior
- Certainty of paternity influences parental care and 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

Fig. 51-21

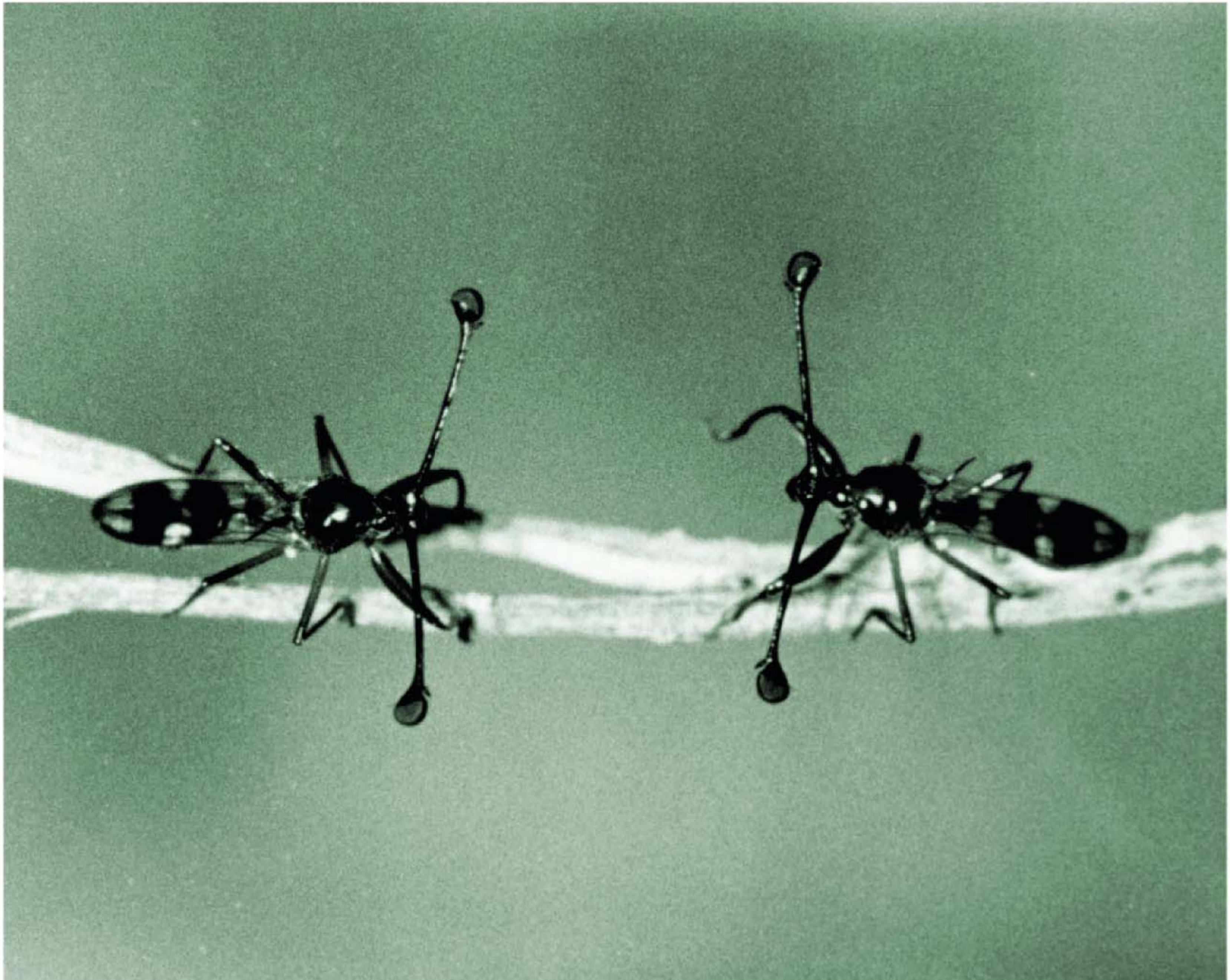
Sexual Selection and Mate Choice

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

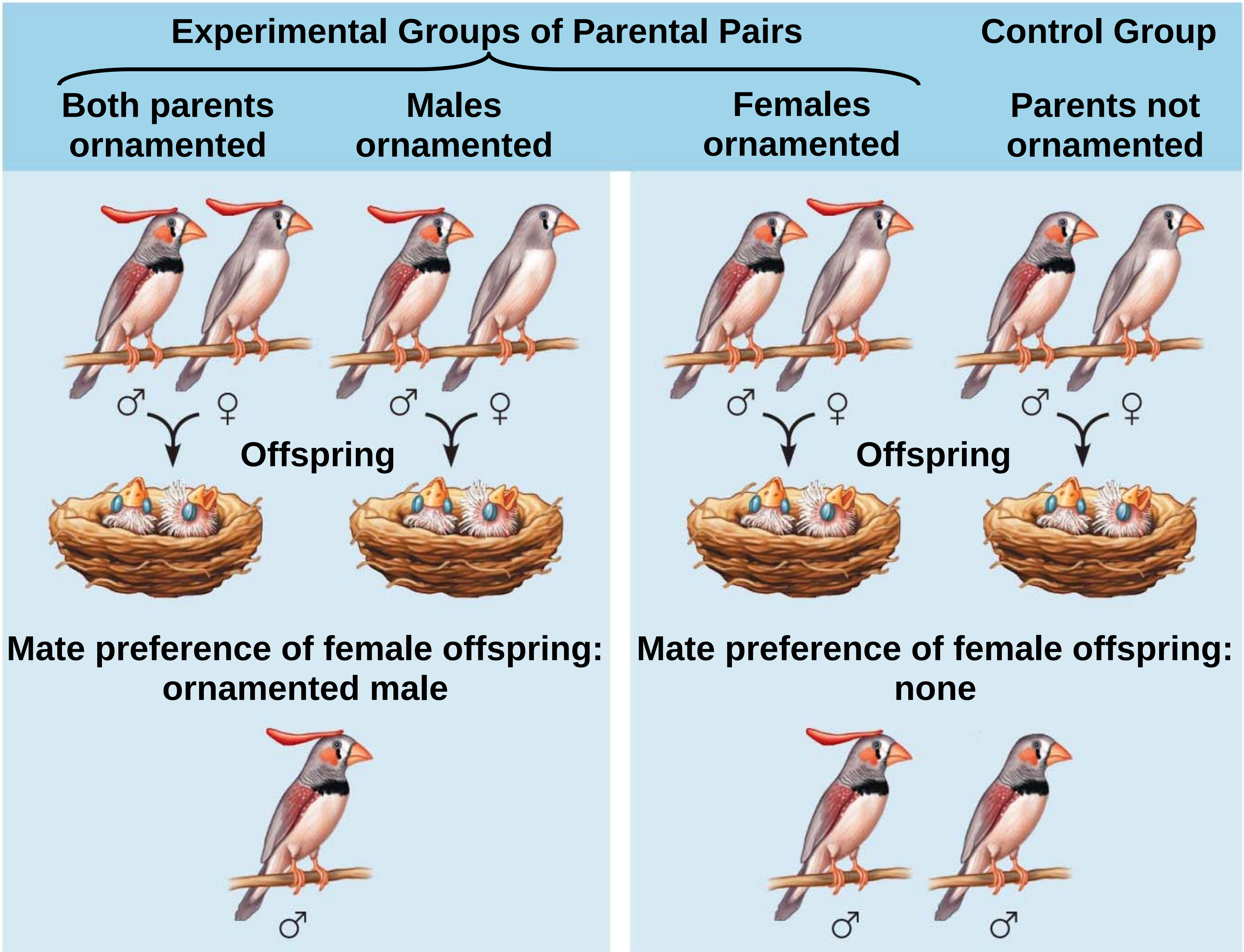
Fig. 51-22



- 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

Fig. 51-23

Fig. 51-24


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

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

Fig. 51-25

PLAY

Video: Chimp Agonistic Behavior

PLAY

Video: Snake Ritual Wrestling

PLAY

Video: Wolves Agonistic Behavior

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, and each color is associated with a specific strategy for obtaining mates
- There is a genetic basis to throat color and mating strategy

- 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

Fig. 51-26

Concept 51.5: Inclusive fitness can account for the evolution of altruistic social behavior

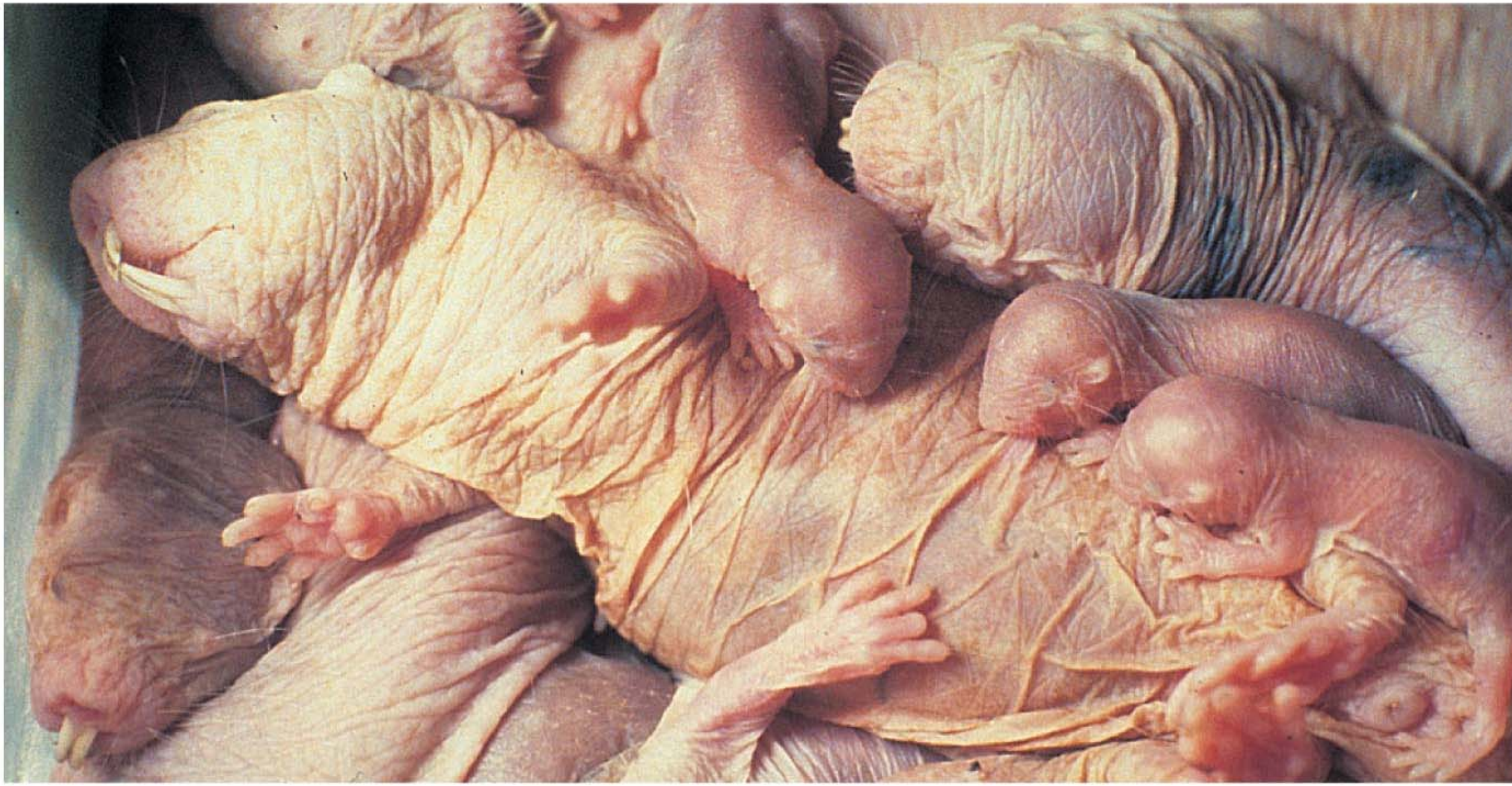
- Natural selection favors behavior that maximizes an individual's survival and reproduction
- These behaviors are often selfish

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
- 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

- In naked mole rat populations, nonreproductive individuals may sacrifice their lives protecting their reproductive queen and kings from predators

Fig. 51-27



Inclusive Fitness

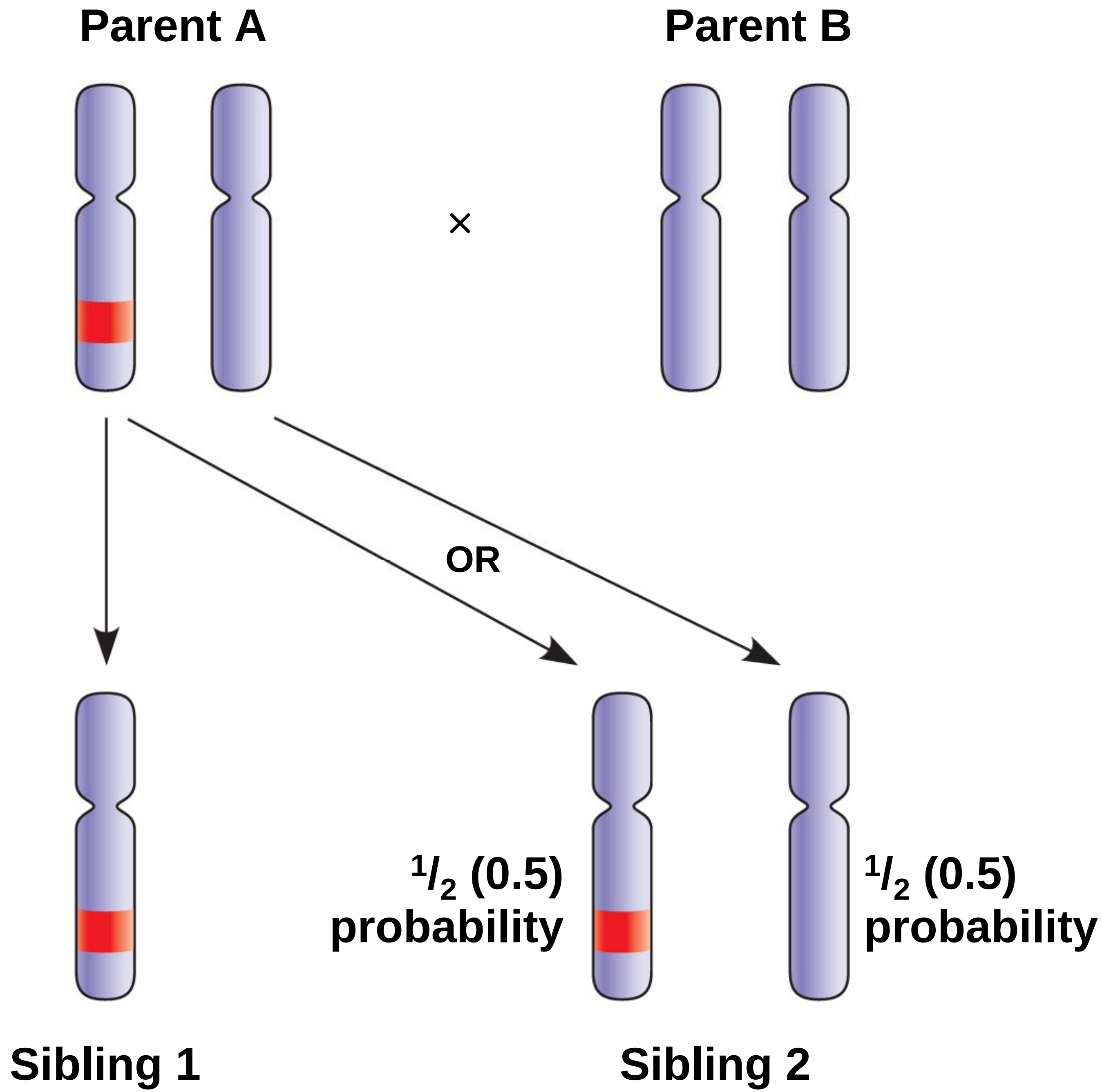
- Altruism can be explained by inclusive fitness
- **Inclusive fitness** is the total effect an individual has on proliferating its genes by producing offspring *and* helping close relatives produce offspring

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 altruist (*C*)
  - **Coefficient of relatedness** (the fraction of genes that, on average, are shared; *r*)

Fig. 51-28


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

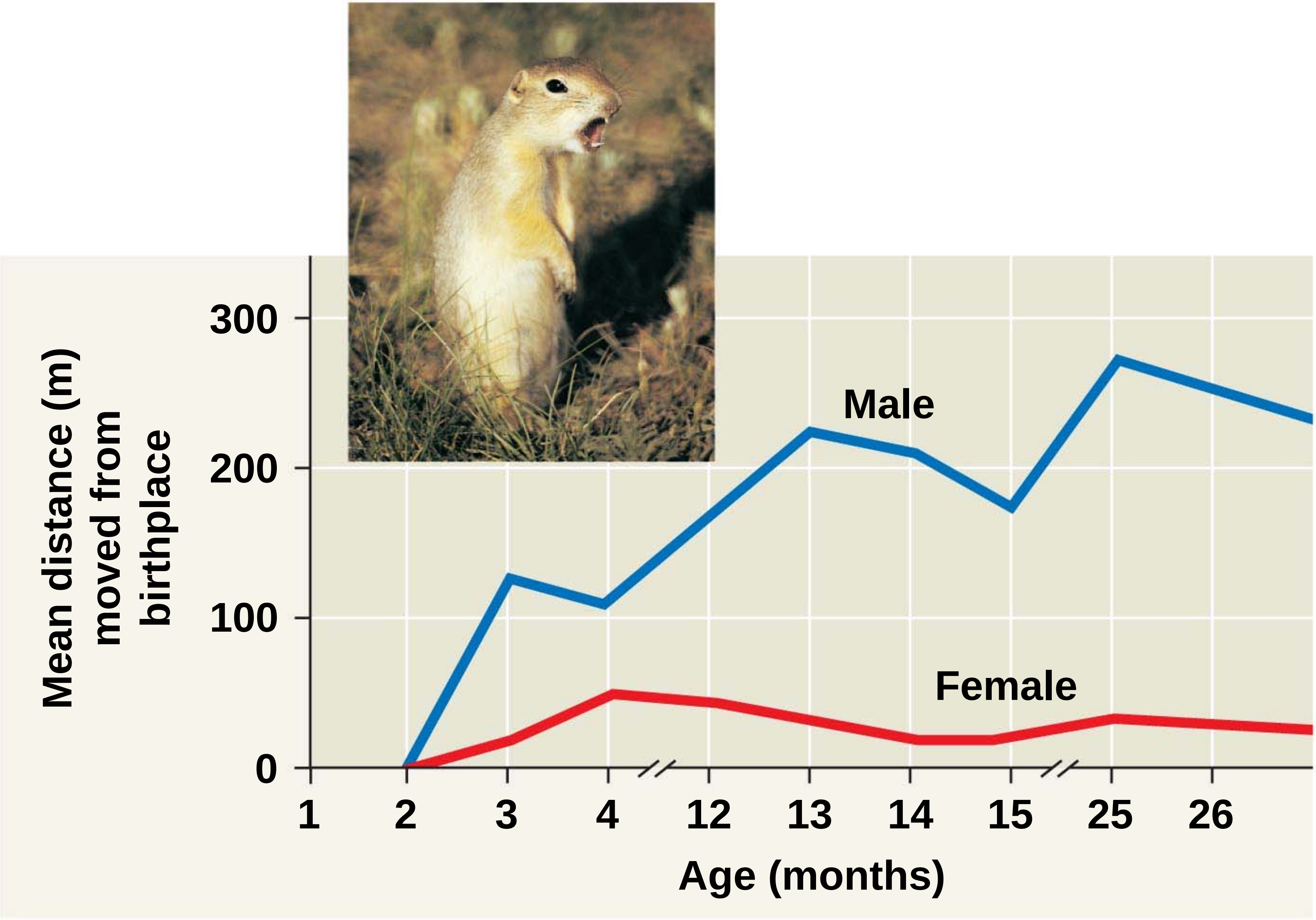
- Natural selection favors altruism when:

$$rB > C$$

- This inequality is called **Hamilton's rule**
- **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

Fig. 51-29



Mean distance (m) moved from birthplace
300
200
100
0
Male
Female
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

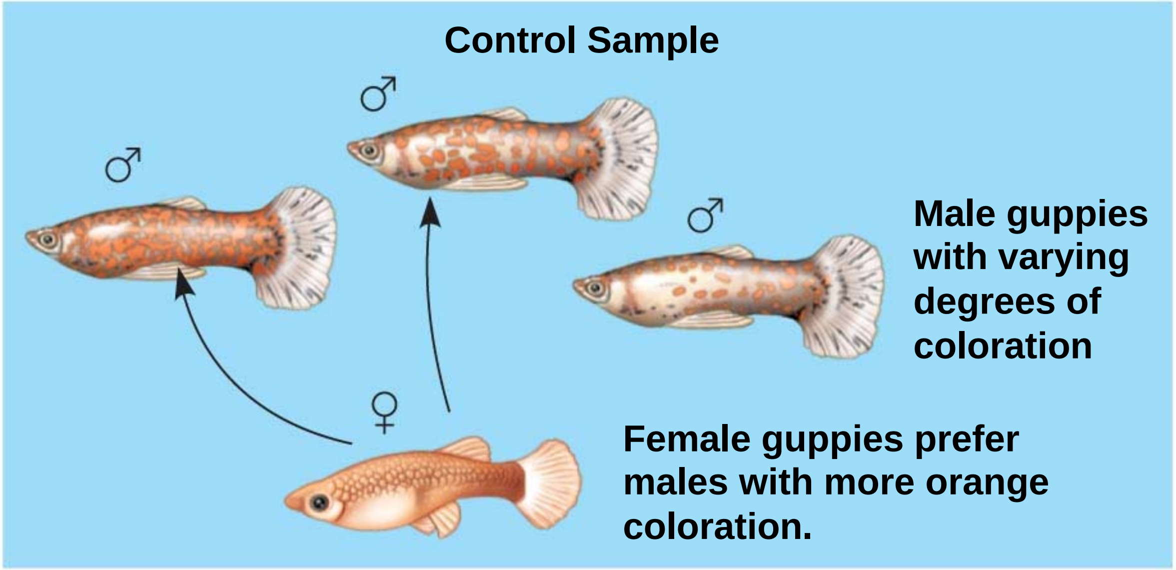
Social Learning

- **Social learning** is learning through the observation of others and forms the roots of culture
- **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

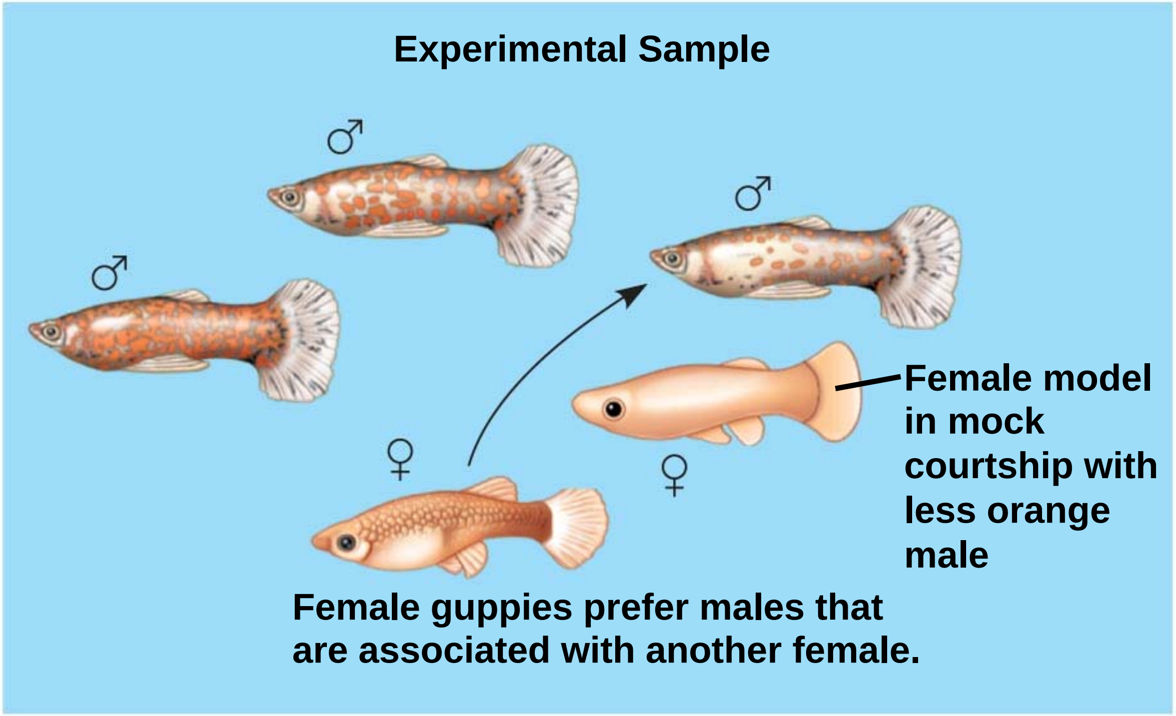
Case Study: *Mate-Choice Copying*

- 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*
- Females who mate with males that are attractive to other females are more likely to have sons that are attractive to other females

Fig. 51-30



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.

Case Study: *Social Learning of Alarm Calls*

- Vervet monkeys produce distinct alarm calls for different predators
- Infant monkeys give undiscriminating calls but learn to fine-tune them by the time they are adults

Fig. 51-31

Evolution and Human Culture

- No other species comes close to matching the social learning and cultural transmission that occurs among humans
- 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

Fig. 51-32

Fig. 51-UN1

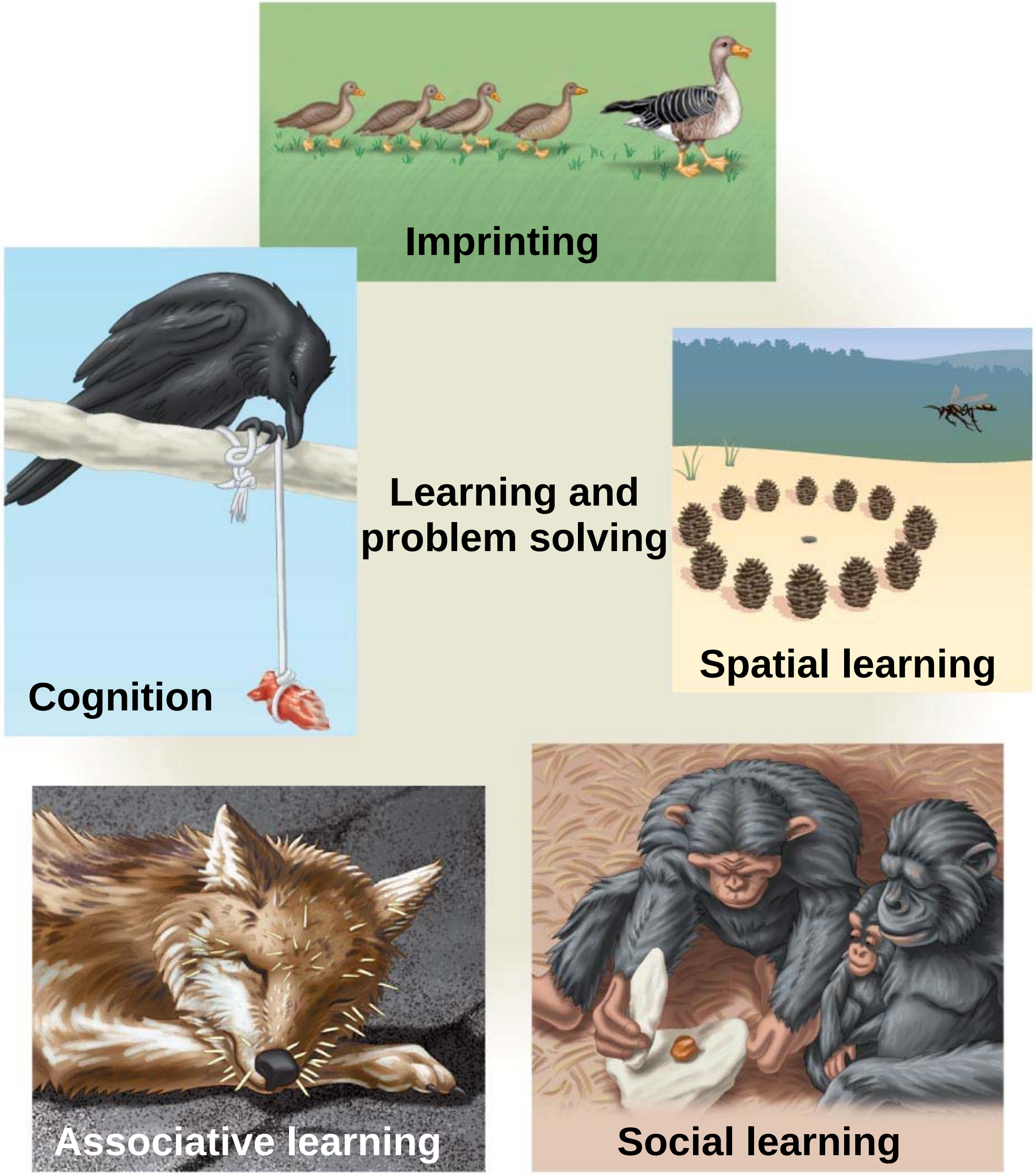
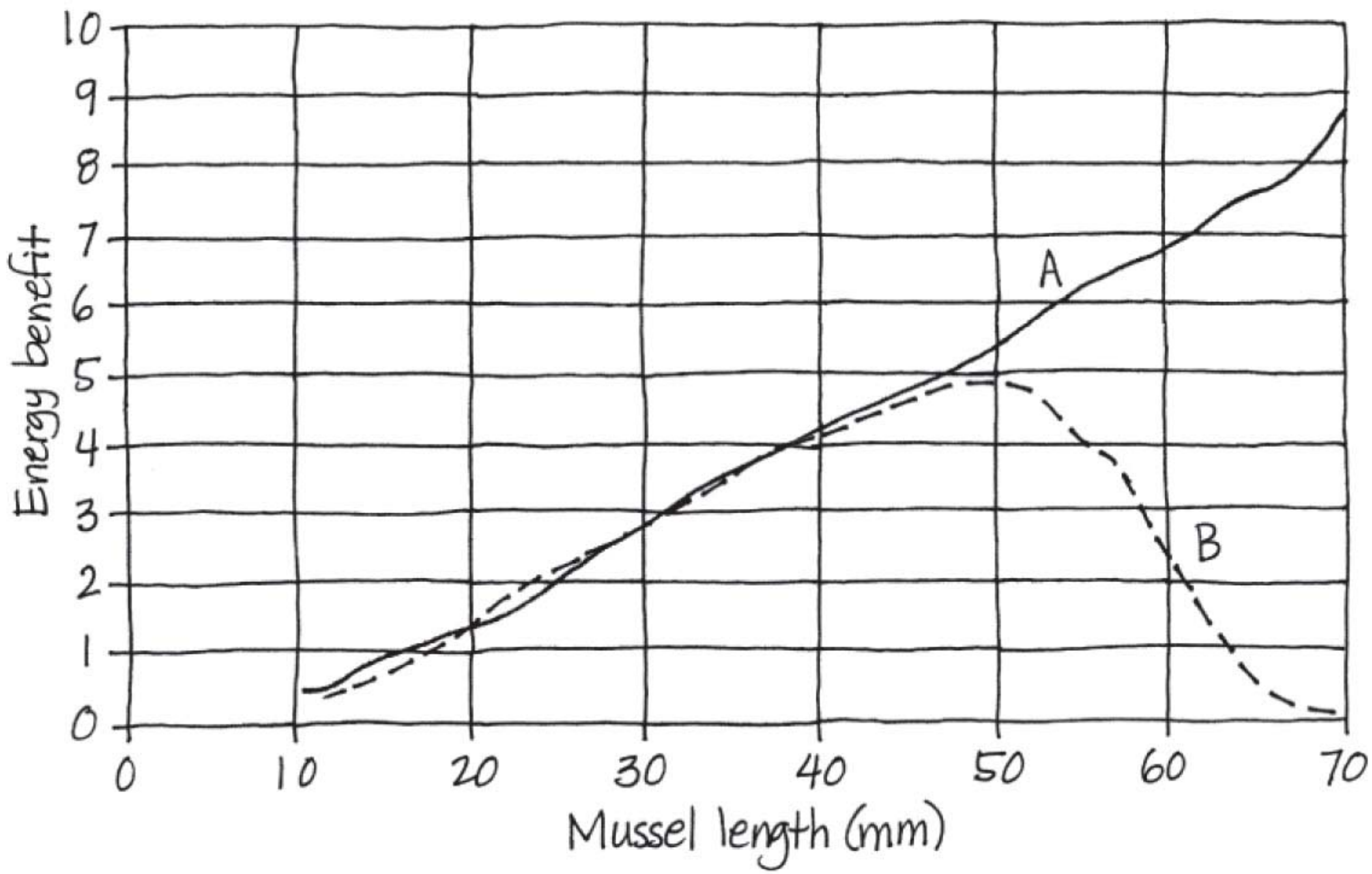

Imprinting
Learning and problem solving
Cognition
Spatial learning
Associative learning
Social learning

Fig. 51-UN2


10
9
8
7
6
5
4
3
2
1
0
Energy benefit
A
B
0
10
20
30
40
50
60
70
Mussel length (mm)

You should now be able to:

1. State Tinbergen's four questions and identify each as a proximate or ultimate causation
2. Distinguish between the following pairs of terms: kinesis and taxis, circadian and circannual behavioral rhythms, landmarks and cognitive maps, classical and operant conditioning
3. Suggest a proximate and an ultimate cause for imprinting in newly hatched geese
4. Explain how associative learning may help a predator avoid toxic prey

5. Describe how cross-fostering experiments help identify the relative importance of environmental and genetic factors in determining specific behaviors
6. Describe optimal foraging theory
7. Define and distinguish among promiscuous, monogamous, and polygamous mating systems
8. Describe how the certainty of paternity may influence the development of mating systems

9. Distinguish between intersexual and intrasexual selection
10. Explain how game theory may be used to evaluate alternative behavioral strategies
11. Define altruistic behavior and relate the coefficient of relatedness to the concept of altruism
12. Distinguish between kin selection and reciprocal altruism
13. Define social learning and culture