Adaptation:
Anti-predator and Foraging Behavior

Why adaptation and anti-predation

Fact – death is bad for fitness

So selection to avoid predation will be intense.

As a result, MANY many anti-predatory behaviors have evolved.

But how did they evolve?

Approach…

Currently the main idea behind behavioral ecology

Historically

- Ethology (study of instinctual behavior in Europe)
- Evolutionary ecology (study of evolution in U.S.A.)

Approach

- Also called the cost-benefit approach
- Choose a behavior of interest
- **Assume** the behavior has an adaptive advantage
  - ie. behavior has been favored by natural selection
  - ie. behavior conveys a net advantage on an animal species
  - Construct a hypothesis about the nature of the adaptation.
  - Or hypotheses about the selective forces that produced the behavior
  - Or hypothesis of “evolutionary design”.
    - Evolution does not have blueprints

Definition

Adaptation

A heritable trait that either spread because of natural selection and has been maintained by selection to the present or is currently spreading relative to alternative traits because of natural selection.

In either case, the trait confers an advantage to those individuals that possess it, which can be translated into **greater reproductive success and fitness**.

Example in Action

Mobbing behavior by black-headed gulls

Why do an activity that expends valuable energy and time, and could result in injury or death?

Does the fitness benefit (+ effect on producing offspring) outweigh the fitness cost (- effect on genetic success)?

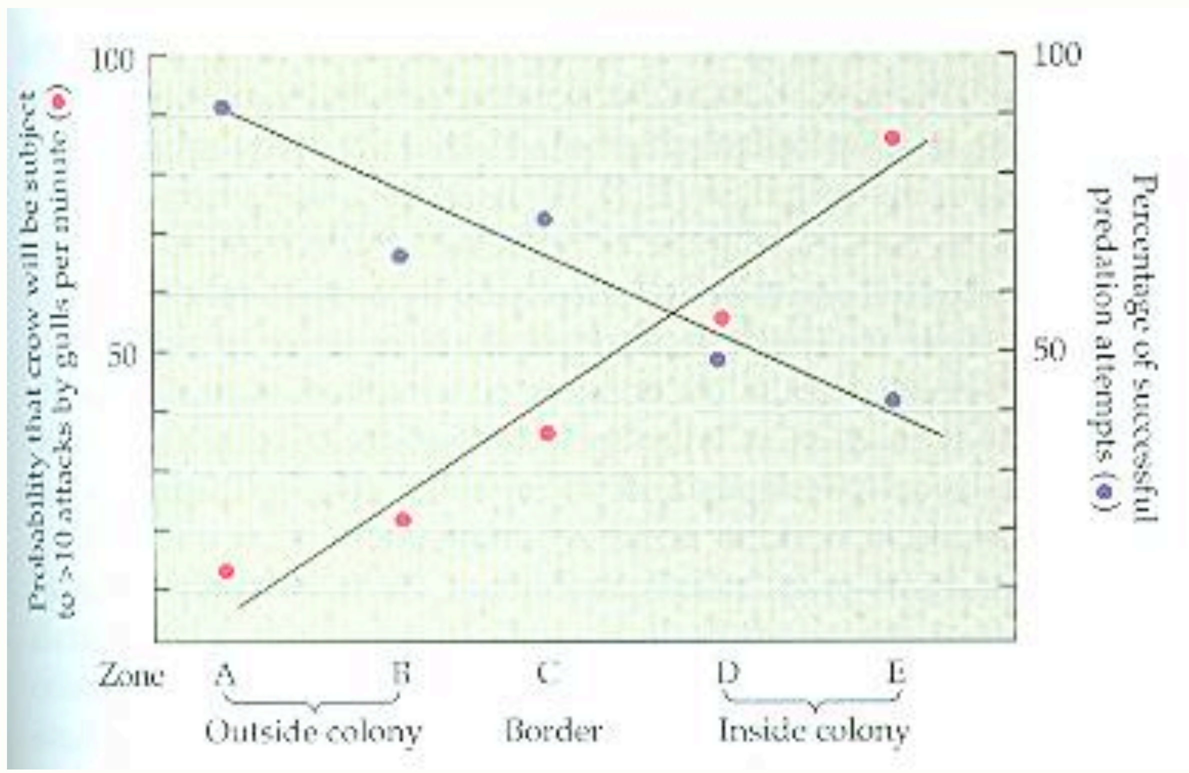
Black-headed gulls

- Gulls are observed to mob (attack) any possible predator that enters their nesting grounds.
- Why attack?
  - To protect yourself
  - To protect your young
- Costs to attacking?
  - Could get injured
  - Could be killed and eaten by predator
- Cost of not attacking?
  - Young get eaten (- reproductive success)

Test the hypothesis

Hans Kruuk tested the predator distraction theory.

Placed 10 eggs, 1 per 10m, along a transect from outside to inside a gull nesting colony.



Comparative Method for Testing

Testing predictions about evolution of a trait by looking at other species.

Start with an ancestral trait for a group, and see where novel difference have arisen.

Determining character states

What is ancestral?

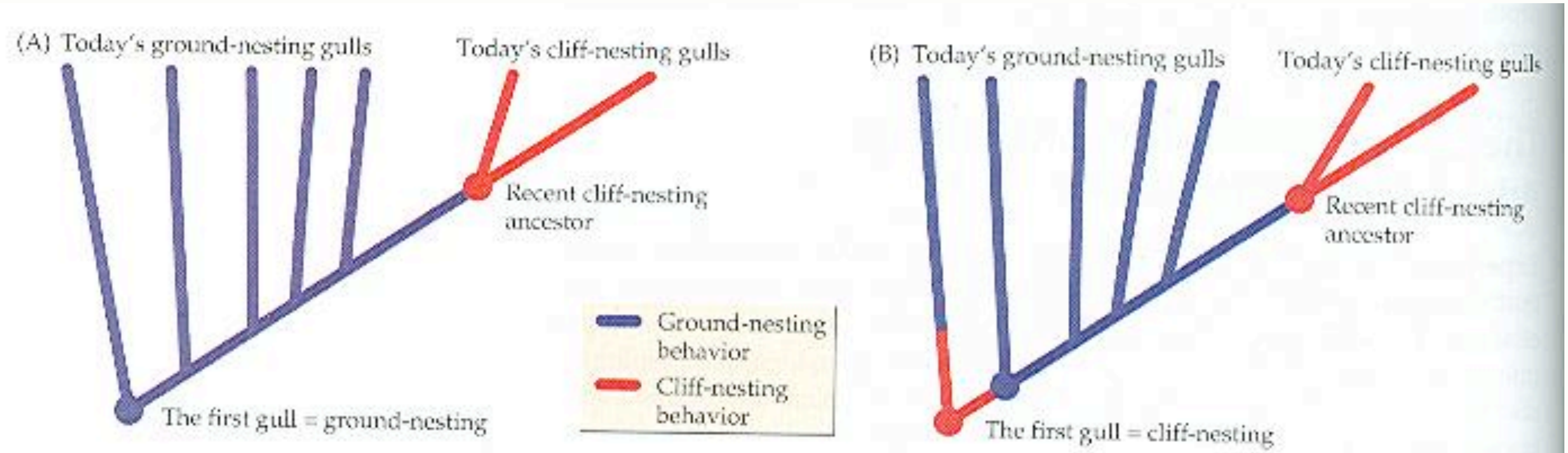
Generally a trait contained by the majority of the group.

Idea that all gulls came from a common gull-like ancestor.

Behavior nesting site.

Most gulls nest on the ground, but a few nest on cliffs.

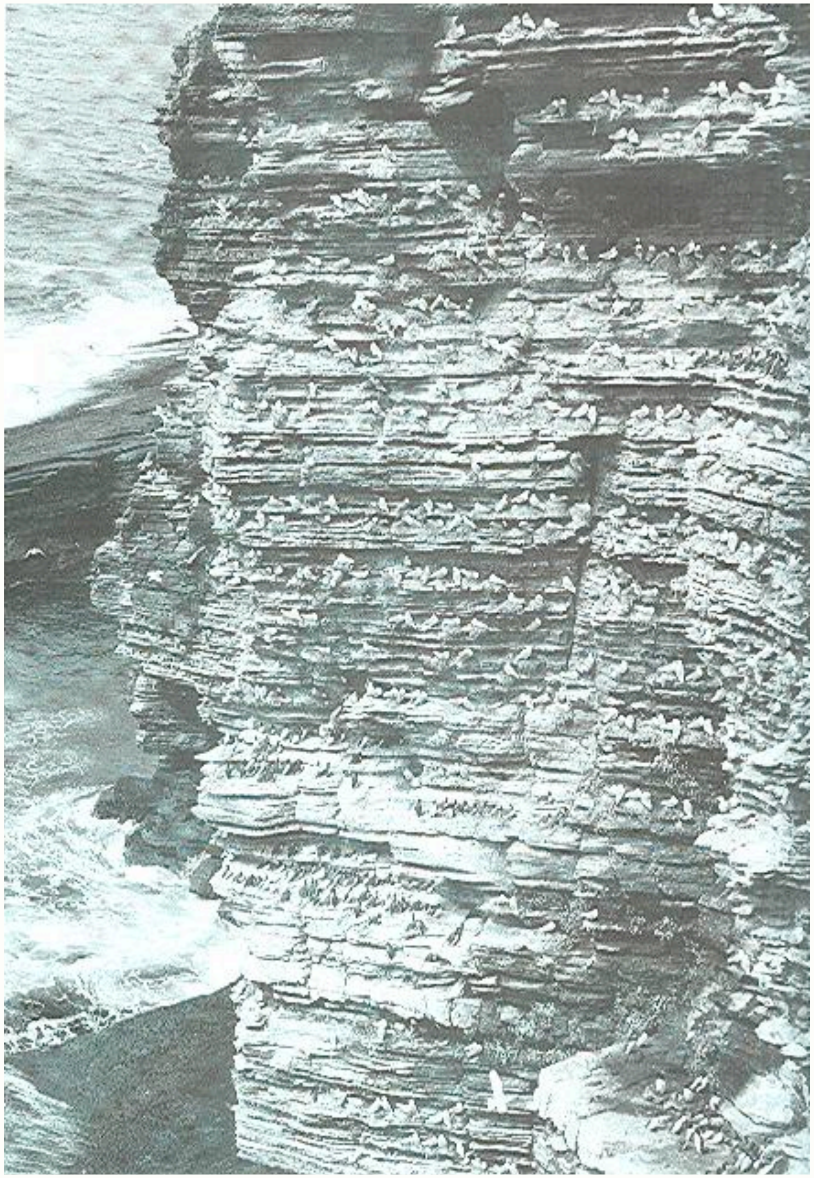
Which is more likely?



4 Gull phylogeny and two scenarios for the origin of mobbing behavior. Hypothesis A requires one switch (from ground-nesting to cliff-nesting); hypothesis B requires two switches (from cliff-nesting to ground-nesting and back again).

Occam's Razor – simpler explanation is most likely correct. (parsimony).

Divergent evolution



Why is a behavior present in most of a group, but not all?

There needs to be a change in the selection pressure for some to promote the success of the new trait.

Kittiwakes have clawed feet to hold onto ledges.

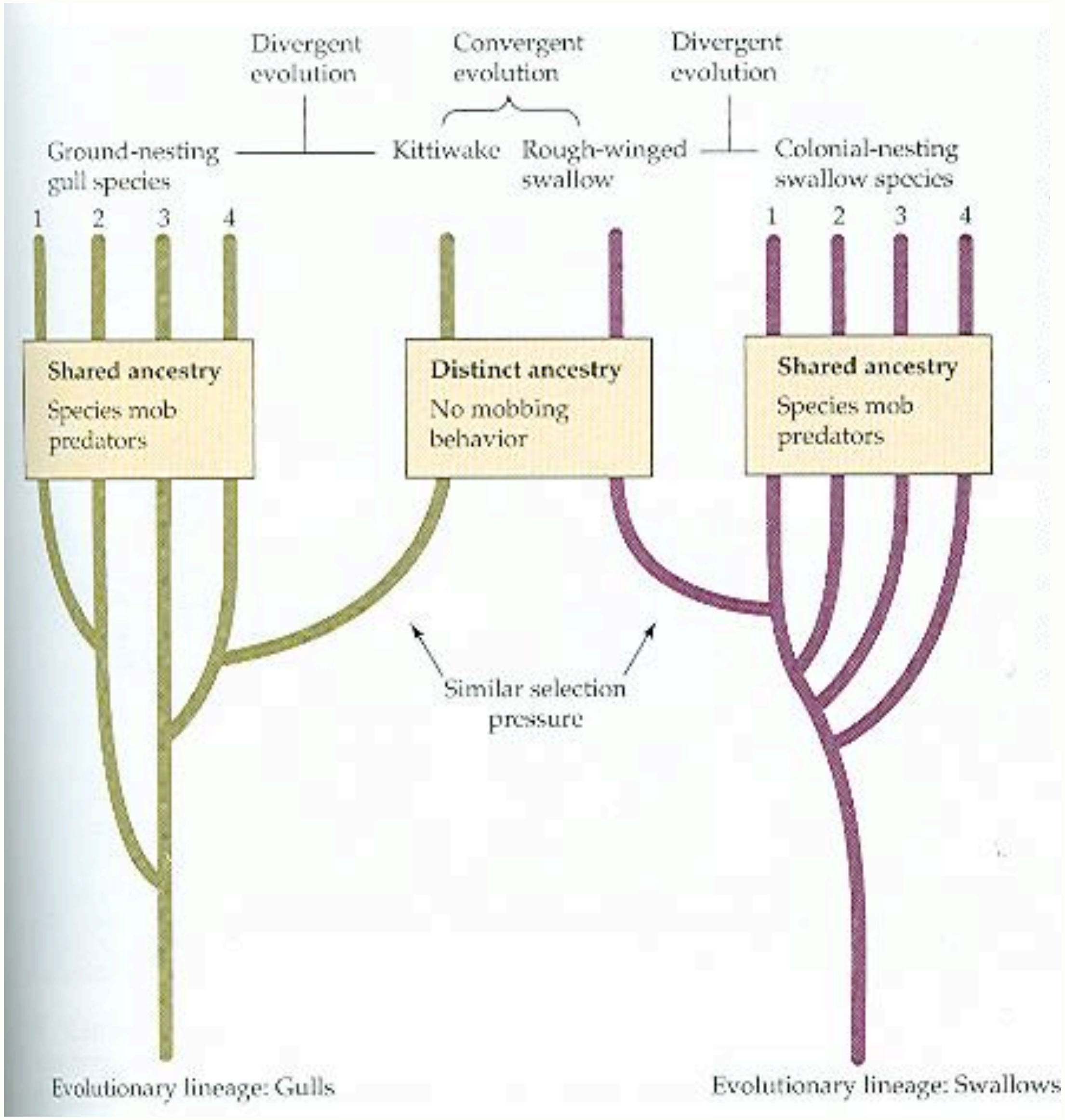
Ledges provide protection from predators of all kinds (mammalian, reptilian, and avian).

Reduced predation pressure has resulted in reduced or zero mobbing behavior.

Convergent Evolution

- Evolution of similar traits by groups that are not evolutionary related but share similar habitats.
- If mobbing occurs in colonial, ground-nesting gulls, then other colonial breeders under predation threats may mob as well.
- This is seen in other bird species, like most sparrows.
  - Some sparrow species are cliff dwelling species, and do not mob predators.

Types of Evolution



Predation Rules the World

Examples and Explanations
of Anti-predatory Behavior

Types of anti-predatory behavior

Decreasing detection by predators

Preventing attack or capture during an encounter with a predator

Behavior once captured

Chemical Defenses

1. Decreasing detection by predators

Major adaptations

Camouflage – matching the background

Behavioral implications

Remain motionless – freezing in presence of possible threat

Behavioral implications

- Remain motionless – “freezing” in presence of possible threat.
- Choose proper location
  - Seems to be the case – animals “realize” their coloration and match background.
- Alter color to match background
  - Lizard (chameleon)
  - Cephalopod (squid and octopus)
  - Fish (flounder)
  - Sunfish and bluegill – takes 2-3 weeks

Cover certain color cells with other cells

Seek Concealment

- Stay in dense vegetation
- Common in small animals
  - Amazon leaf-carrying fish
  - Song birds moving within brush or cover

Removing evidence of presence

- Tinbergen’s egg shell experiments
- Birds remove egg shell from nest after young hatch.
  - Avoid detection by predators
- Caterpillars
  - Chickadees learn that damaged leaves have caterpillars
  - A “clever” caterpillar eats around the edge to make leaf look undamaged
- Anti-predatory behavior
  - trim edges, clip damaged leaves, leave leaf during the day

Clever Caterpillars and Chickadees

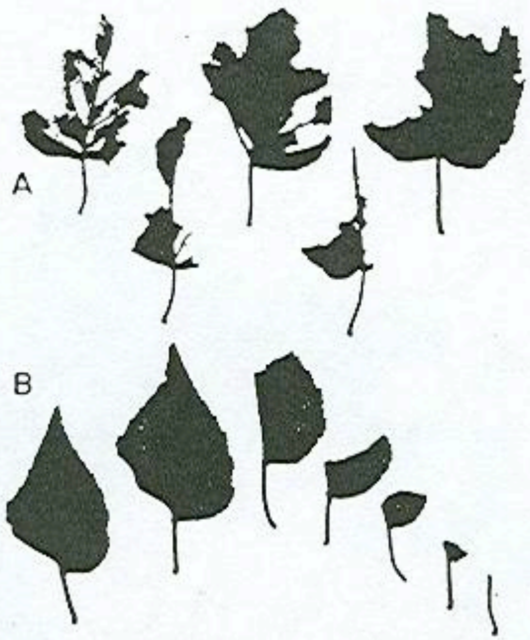
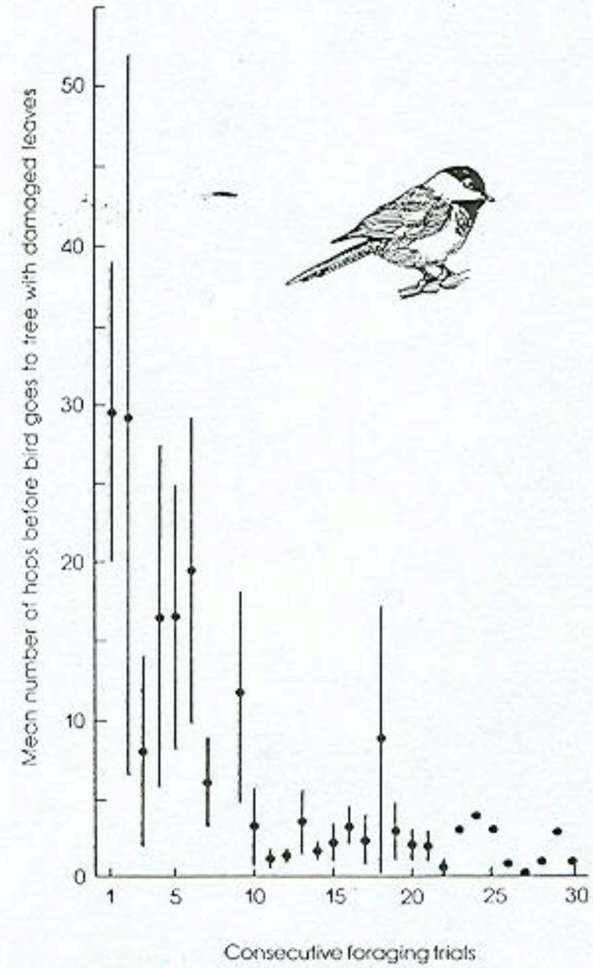


Figure 7.10. Representative leaf damage and feeding sequence on birch. (A) The spotted halysidota, *Halysidota maculata* (Arctiidae). (B) *Heterocampa* sp. (Notodontidae) showing a leaf trimmed and consumed in stages (left to right).



CHICKADEES LEARN TO VISIT DAMAGED LEAVES if those leaves have prey on them. The mean number of hops before captive birds went to a tree with damaged leaves in an enclosure declined rapidly as the chickadees learned to associate this cue with food rewards.

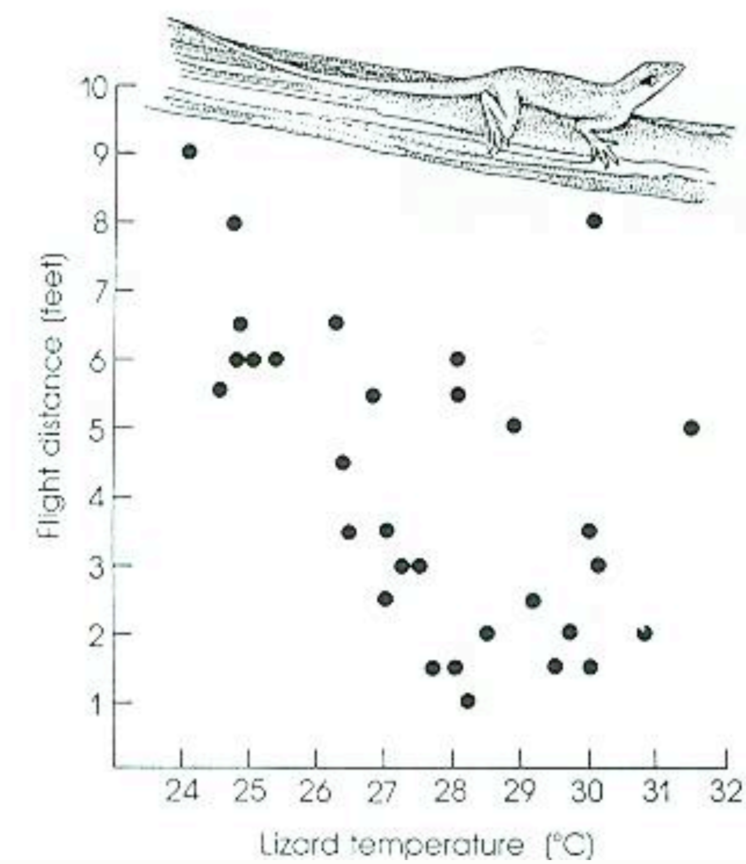
2. Preventing Attack or Capture

When to initiate escape?

- Decide when or whether you need to initiate escape
- Escape can be costly in time and energy.

Ex. Lizard flight initiation distances

- When warm, will allow threat to get closer
- Main tactic is actually cryptic coloration and stillness, run only when believed discovered.



Pursuit deterrence signal

- An honest signal of ability to escape.
  - "I can run away…don't even bother."
- Ex. Stotting in gazelles
  - Jumps really high
- Hypothesis 1 – signal to other gazelles
  - Alarm
  - Group formation
- Hypothesis 2 – Pursuit-deterrence signal

Stotting and Signals

Observations: stotting observed in solitary gazelles

- Also flash white hind quarters to predator
- Predator generally abandons chase when stotting (3/4 of the time).

White-tail deer in North America also stott and flash tail to say “Hi, I see you.”

Tail wagging in lizards also the same signal.

Protean Behavior

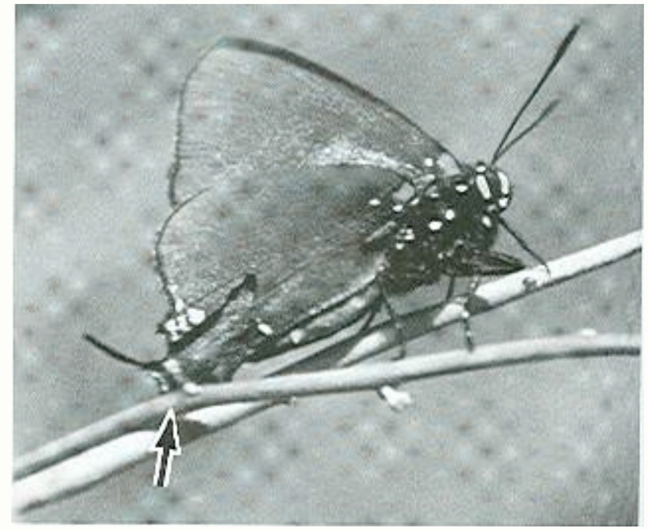
Extremely erratic behavior during escape

Random turns and reversals (zig zag)

This is common in many animals, occurs when you are about to get caught.

6.15 Cryptic coloration depends on background selection

Misdirecting Attacks



- False heads
- Fish have false eye spots
- Tail loss in lizards
    - Ability to jettison tail to escape capture. Can re-grow it later.

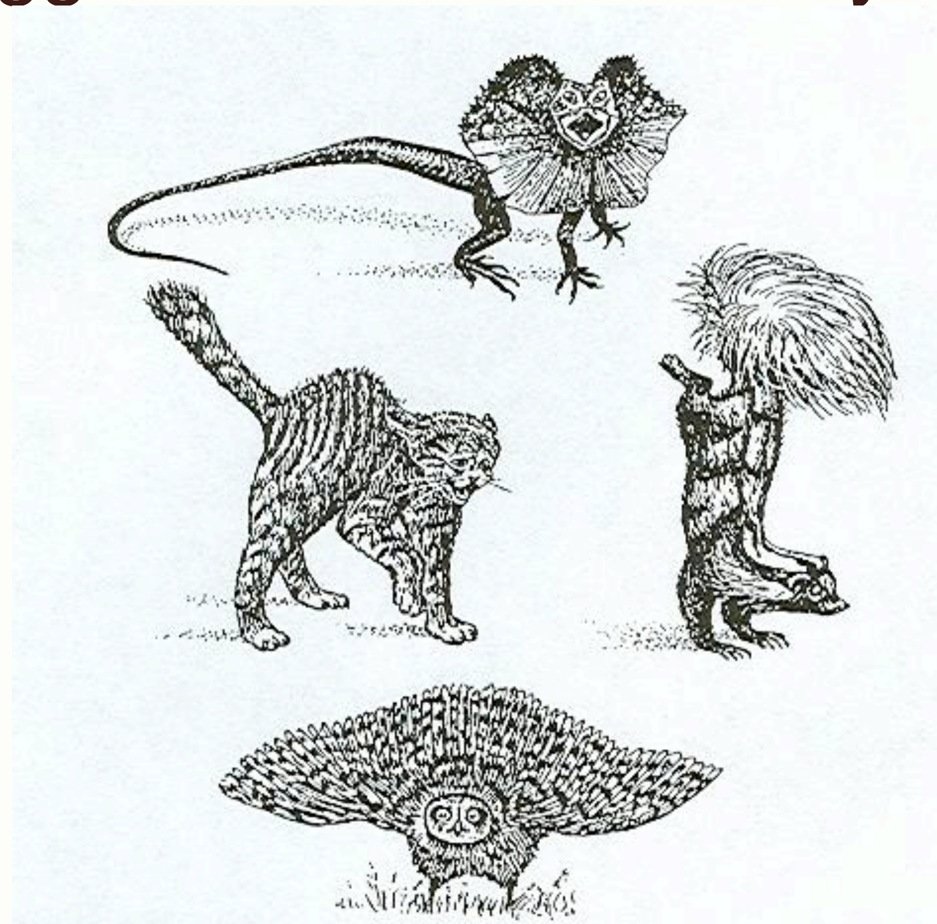
Distraction Displays

Attempt to look injured to lure predator away from young.

Generally in shorebirds (Killdeer)

Intimidation Displays

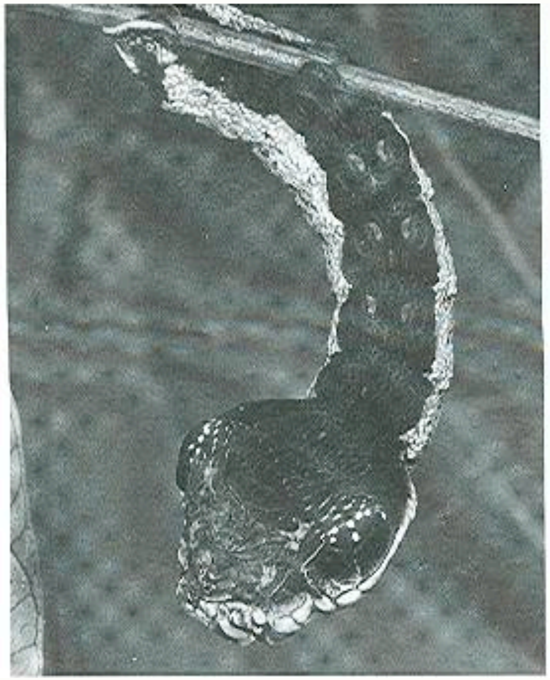
Look bigger and meaner than you are.



Startling Displays

- Deter attack
- Gain time for escape
  - Ex. Moth eye spots
    - Gives them time to escape
  - Toad w/ 2 black spots that blow up when threatened
  - Caterpillars that can inflate and look like a snake
  - Fly wings that resemble spider legs
  - Birds will fly right at the predator as a last resort (Hans Solo maneuver)

Startling Displays



Predator Inspection Behavior

- Approach predator
- A form of pursuit deterrence in some cases.
- Lets the predator know its been seen
- May also get info on the predator
  - Identity of predator
  - Identify state of predator (whether its hunting or not)

3. Behavior Once Captured

- Fight back
- Fear screams upon capture
  - Warns others (relatives) when self dies
  - Might startle predator (not effective)
  - Get help
  - Attract other predators. Why???

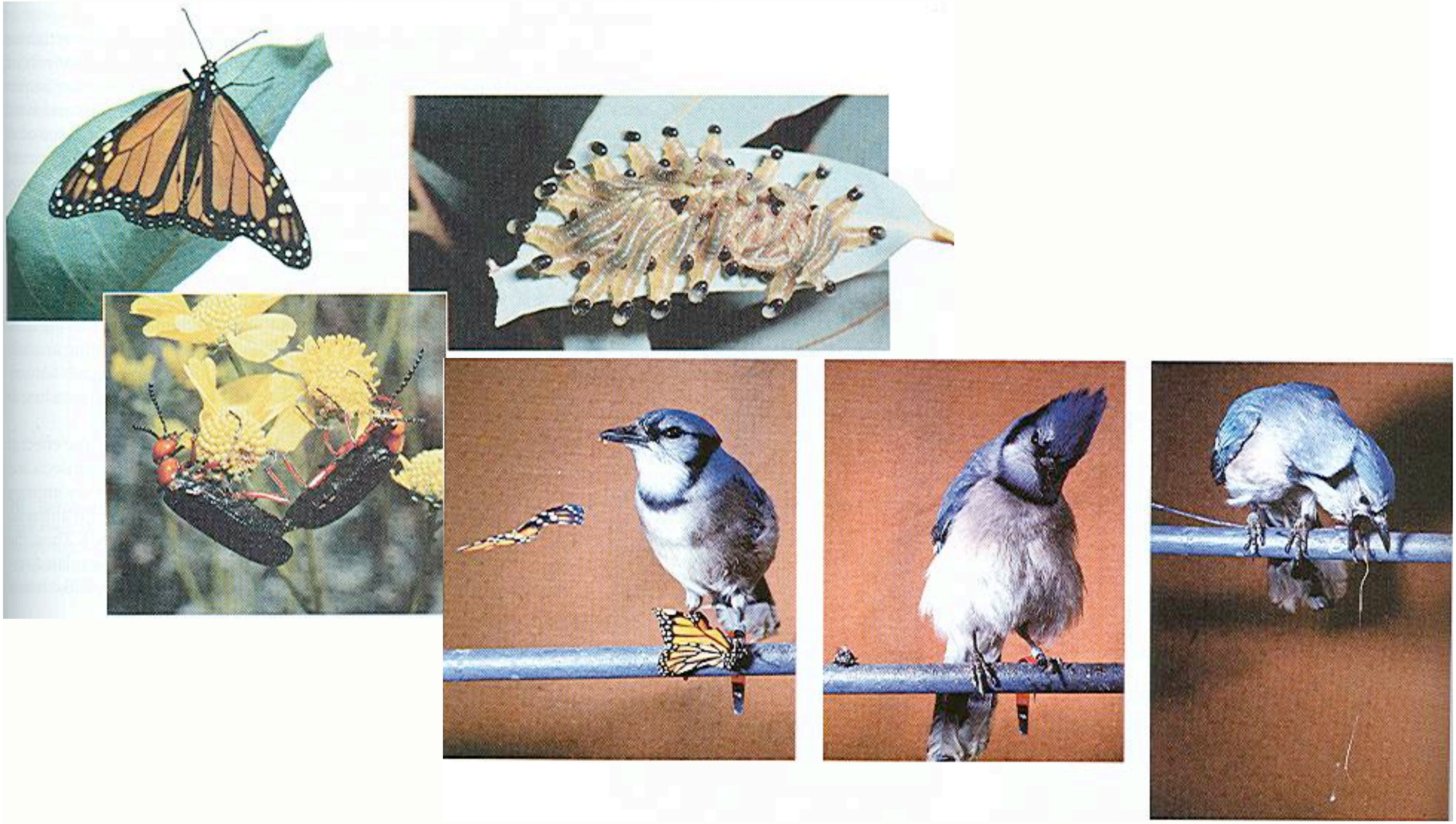
Behavior Once Captured

- Other predators might fight over you, giving you a chance for escape.
  - Best studied in birds.
- Play Dead
  - Predator might let go
  - May ignore prey
  - “Tonic immobility” – going limp and play dead.

4. Chemical Defenses

- "Slime and Goo" defenses
  - Black widow spider
  - Salamanders
  - Termites (part of gooey head blows up)
- Noxious defenses
  - Skunks
  - Poison skin (frogs and toads)
  - Stinging insects (bees and ants)
  - Monarch butterflies (toxin from plants)

Chemical Defenses



Deception – Batesian mimics

Aposematically colored animals that are not toxic

Bee-fly mimics

19 Batesian mimics resemble other species that are protected against predation. Although these insects look like (left) a bee, (middle) a yellow-jacket wasp, and (right) a paper wasp, they are actually all harmless flies. Photographs by the author.

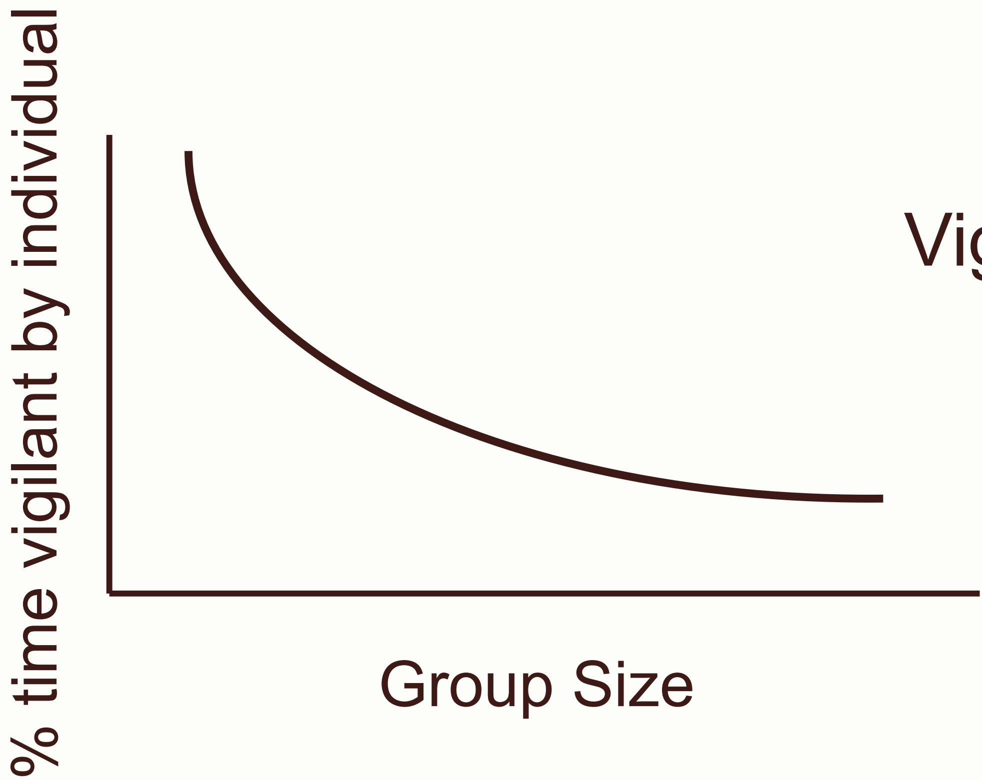
Acoustical mimic

Burrowing owls can make a rattle sound like an rattlesnake.

Social Defenses

- Group intimidation of predators
  - Muskox and buffalo
  - Some moth and sawfly larvae practice group vomiting
- Improved predator detection in groups
  - Extremely common benefit to grouping in vertebrates
  - In a group – there are more eyes looking for predators
- Assumption : a detector has to be able to warn others of attack through either alarm call or behavioral change

Many-eyes effect



Vigilance – time spent alert

Effect of many eyes

Vigilance goes down as group size increases

Time spent foraging therefore goes up as group size increases

Even though individuals are less vigilant, the group has a high collective vigilance.

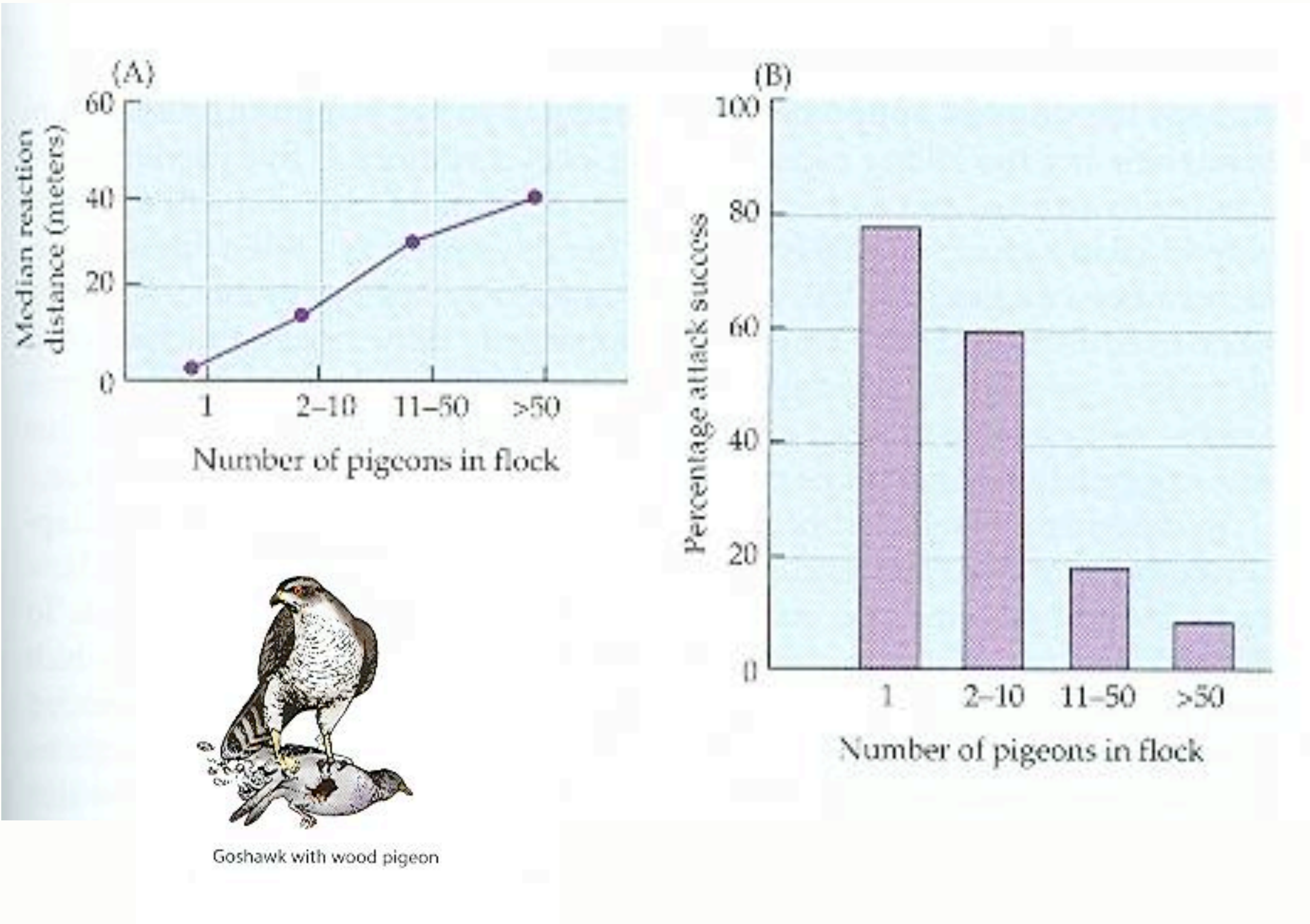
- Only works if everyone in groups will get the warning.

Table 4 Effects of group size on the response of caged starlings to a simulated predator

	Number of starlings in cage	
Behavioral effect	One	Ten
Mean number of times per minute that bird stops foraging to look up	23.4	11.4
Percentage of foraging time spent in surveillance	47	12
Mean takeoff time (seconds) after hawk model is released	4.1	3.2

Source: Powell [955].

Vigilance against hawks



Selfish herd effect

Animals seek the safest position within a group

Safest location is in the center, all else equal.

Dominate individuals are commonly in the center (largest)

Examples of selfish herds

Ex. Schools of fish

- Cost of protection – food is less plentiful
- Increased competition for food
- Hungry individuals are on the outside or edge of the group

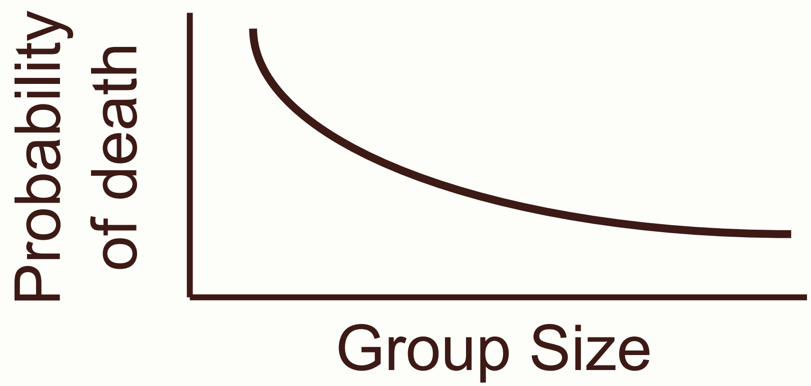
Ex. Penguins

- If a seal is attacking, the dominate penguins in the center push others off the ice to feed the seal.

Dilution of risk (numerical dilution)

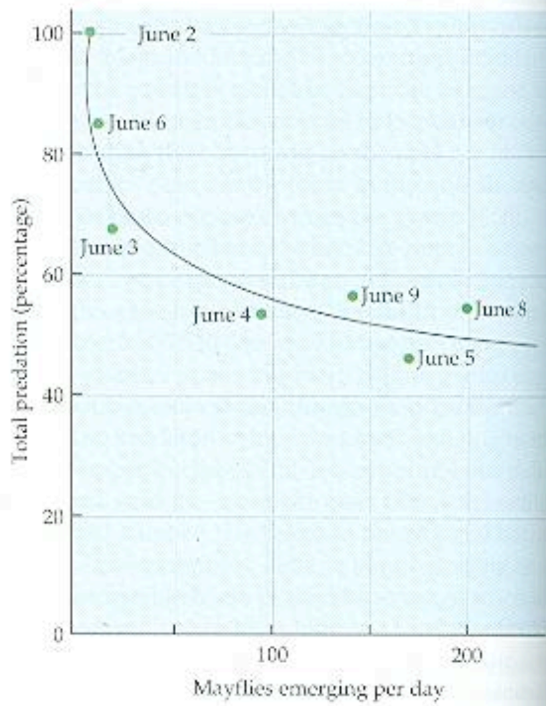
When an attack is successful, what is the probability of being killed.

The probability of death = 1/N (group size).



Dilution effect may favor synchrony in reproduction in colonial animals

Mass Reproduction/Hatching



26 The dilution effect in mayflies. The more female mayflies that emerged together on a June evening, the less likely any individual mayfly was to be eaten by a predator. After Sweeney and Vannote [1118].

Adaptive Feeding Behavior -- Chapter 7

ANIMAL BEHAVIOR, *Eighth Edition*, Chapter 7 Opener

The Truth of Life

- All animals consume food and are potential food for others
- These two facts shape behavior
  - Efficient predators
  - Animals that assess risk of being killed while feeding

Locating Prey

1. Methods of Detection
2. Search Image Formation
3. Social Location of Food
4. Local Enhancement Effect

Methods of Prey Location

Different organisms rely on various methods for finding food.

Invertebrates

- Tactile, chemical (olfaction)

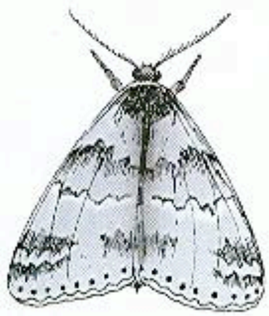
Vertebrates

- Vision, olfaction, hearing

Search Image Formation

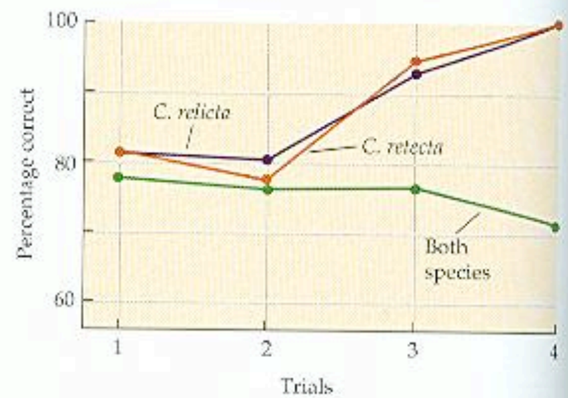
Learn to see cryptic prey

- Blue jay forms search image for simple things quickly.
- Complicated searches (multiple species) take longer to learn
  - Most prey are cryptic



Catocala relicta

Catocala retecta

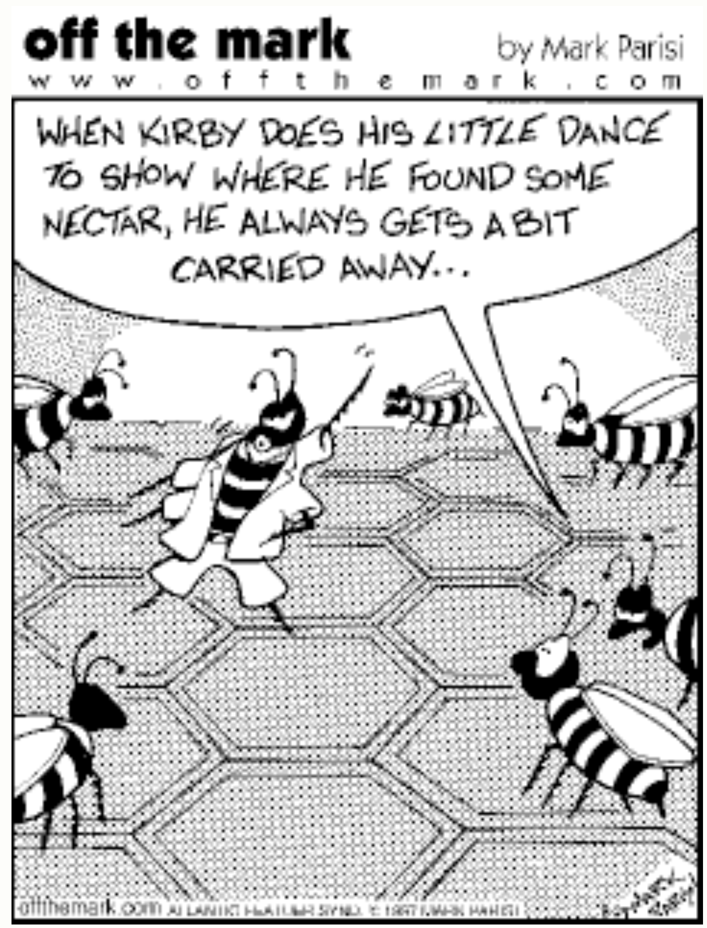


1 Search image formation in blue jays. When given the task of detecting moths that appeared in 8 of 16 slides, blue jays did not improve over the course of the test if there were 4 slides of one moth species and 4 of another species intermingled in the series. But if all 8 slides showed just one moth species, the jays' moth detection scores improved, suggesting that they had learned to search for the key cues associated with that species. After Pietrewicz and Kamil [918].

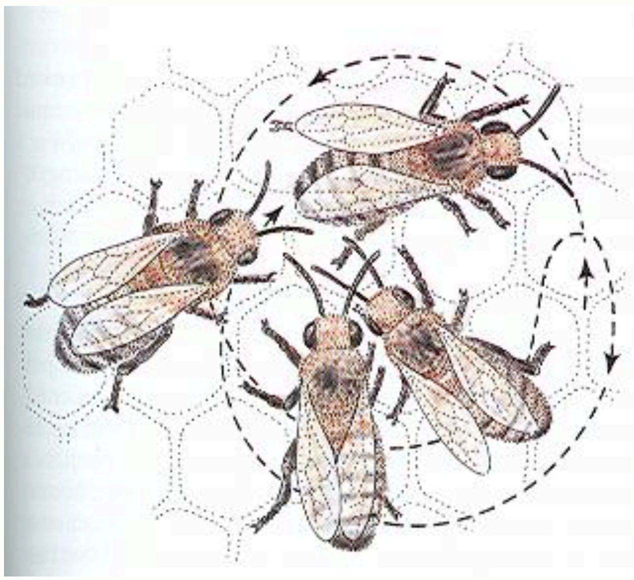
Social Location of Food

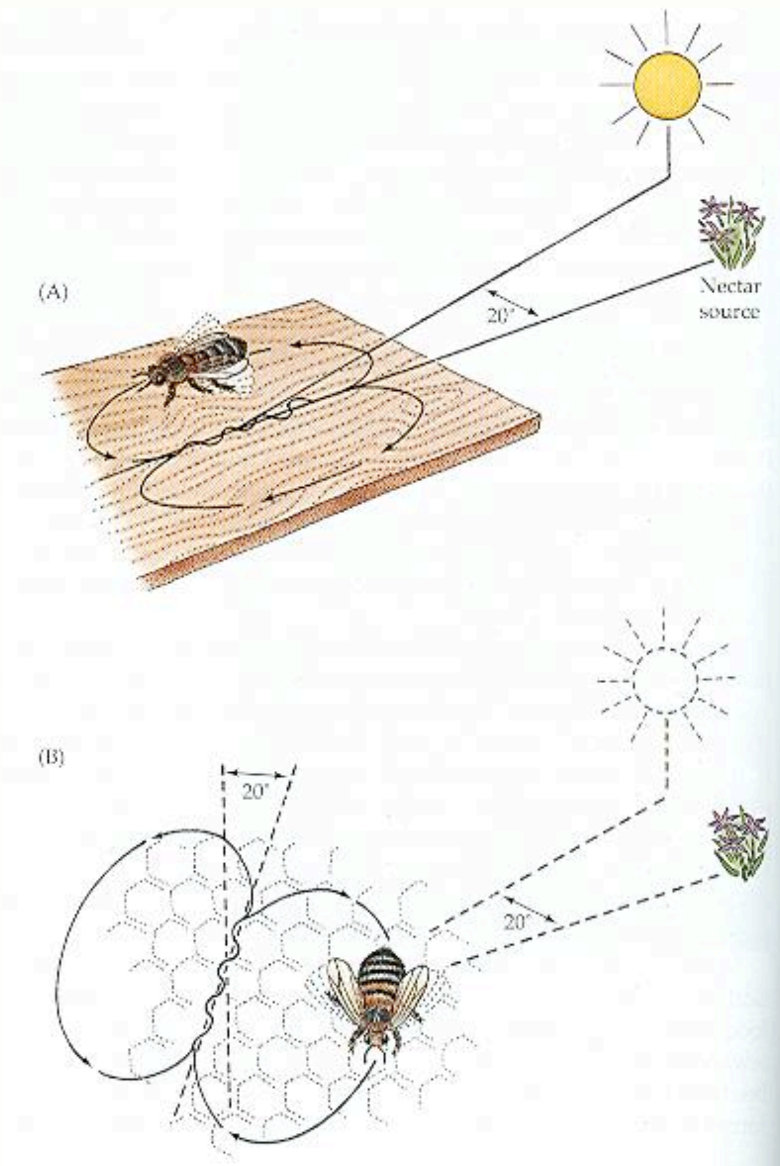
Honey bee work by Karl von Frisch

How do bees convey information about valuable food resources in the dark of the hive?



Circle and Waggle Dances





Information of the dance

The type, duration, and angle of the dance provide information.

Round dance = < 50 m

Waggle dance = > 50 m

Duration/length = distance to food

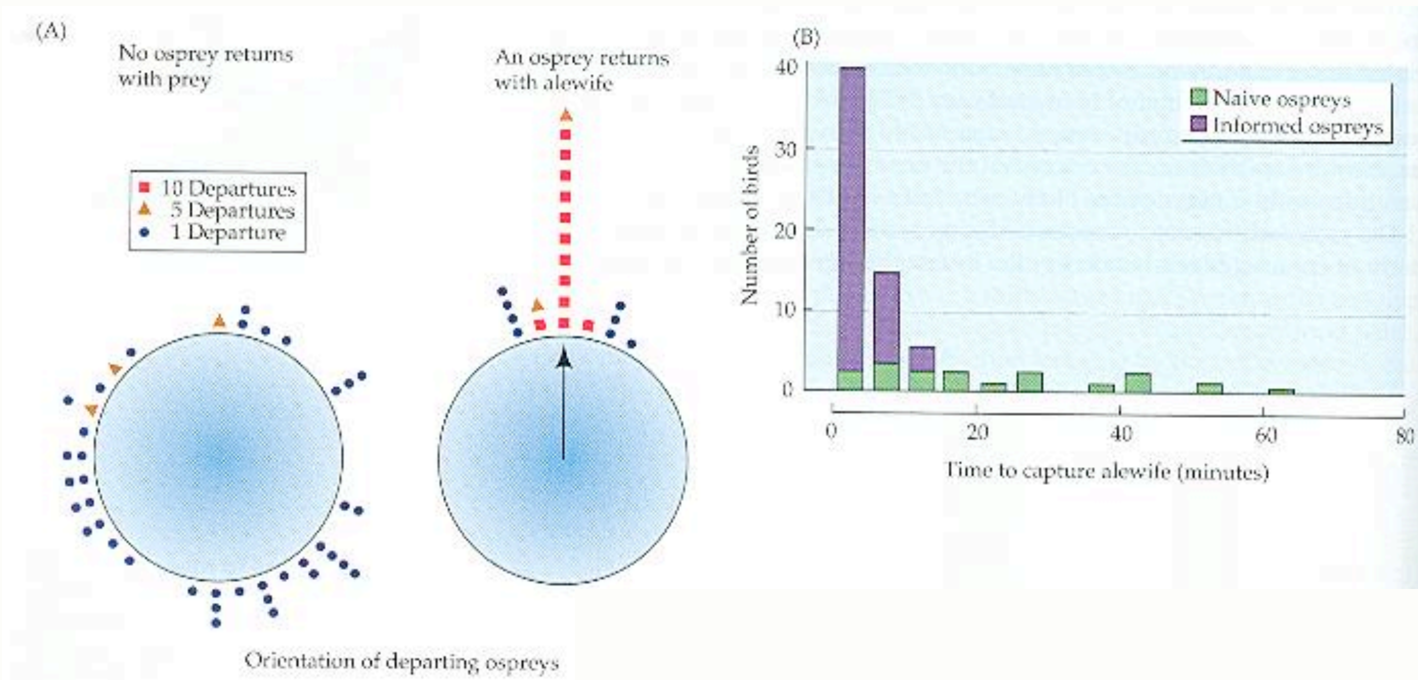
Angle off the vertical = angle of the sun

Intensity = abundance of food

Information Center Hypothesis

Colonies or social roosts serve as a source of information that can be used by members.

Ex. Ospreys



Local Enhancement Effect

Animals are attracted to other actively feeding animals.

Not an information center idea

- Actually see feeding activity

Ex. Vultures and gulls

Prey Capture

Hunting Modes

Capture Techniques

Cooperative Prey Capture

Prey Capture

Capture can be trivially simple

- Seed and fruit eaters

For larger predators, capture can be very difficult.

- Mobile prey capable of escape

Hunting Modes

Ambush mode

- Sit and wait
  - Snakes and many lizards (*Phrynosoma*)

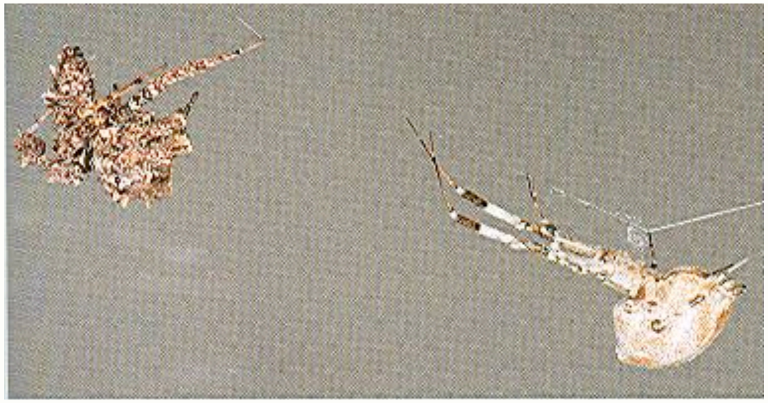
Pursuit mode

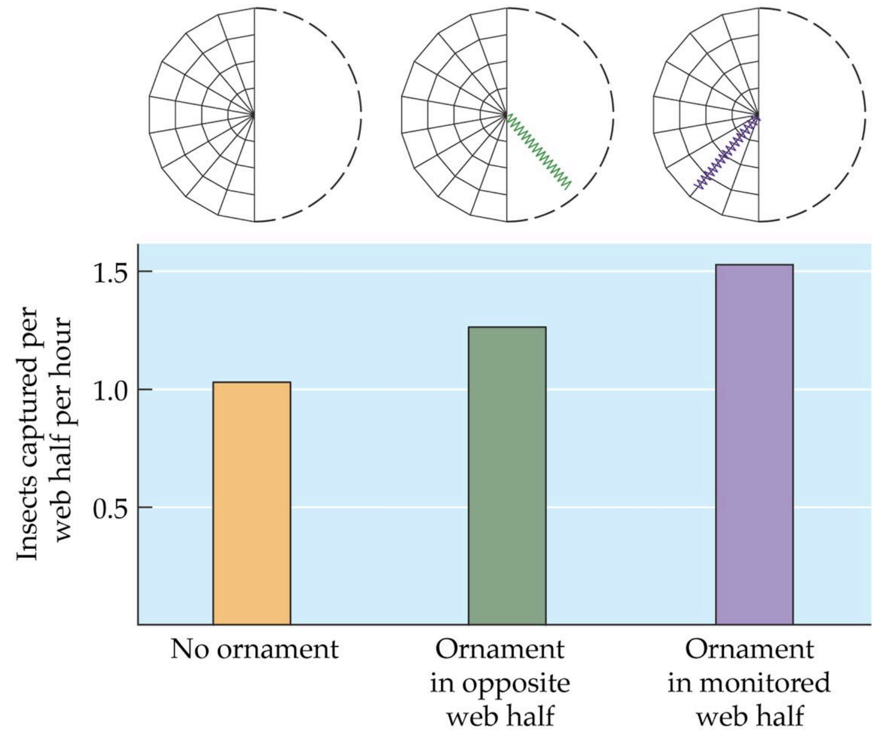
- Active searchers
  - Wild dogs

Capturing Techniques

- Grab
- Poison
- Traps
    - Spiders
- Deceptive lures
    - Snapping turtle
        - tongue

Spiders and deception





ANIMAL BEHAVIOR, Eighth Edition, Figure 7.15 © 2005 Sinauer Associates, Inc.

7.16 Some spiders appear to hide

Cooperative Prey Capture

- Rare in the animal world
  - Why?
- Several independent evolutionary origins
  - Ex. Vertebrates (lions, canids, mustelids, some birds
  - Ex. Invertebrates (Hymenopterans)

Cooperative Prey Capture

Benefit:

- Capture large prey
- Capture nimble prey
- Defend prey

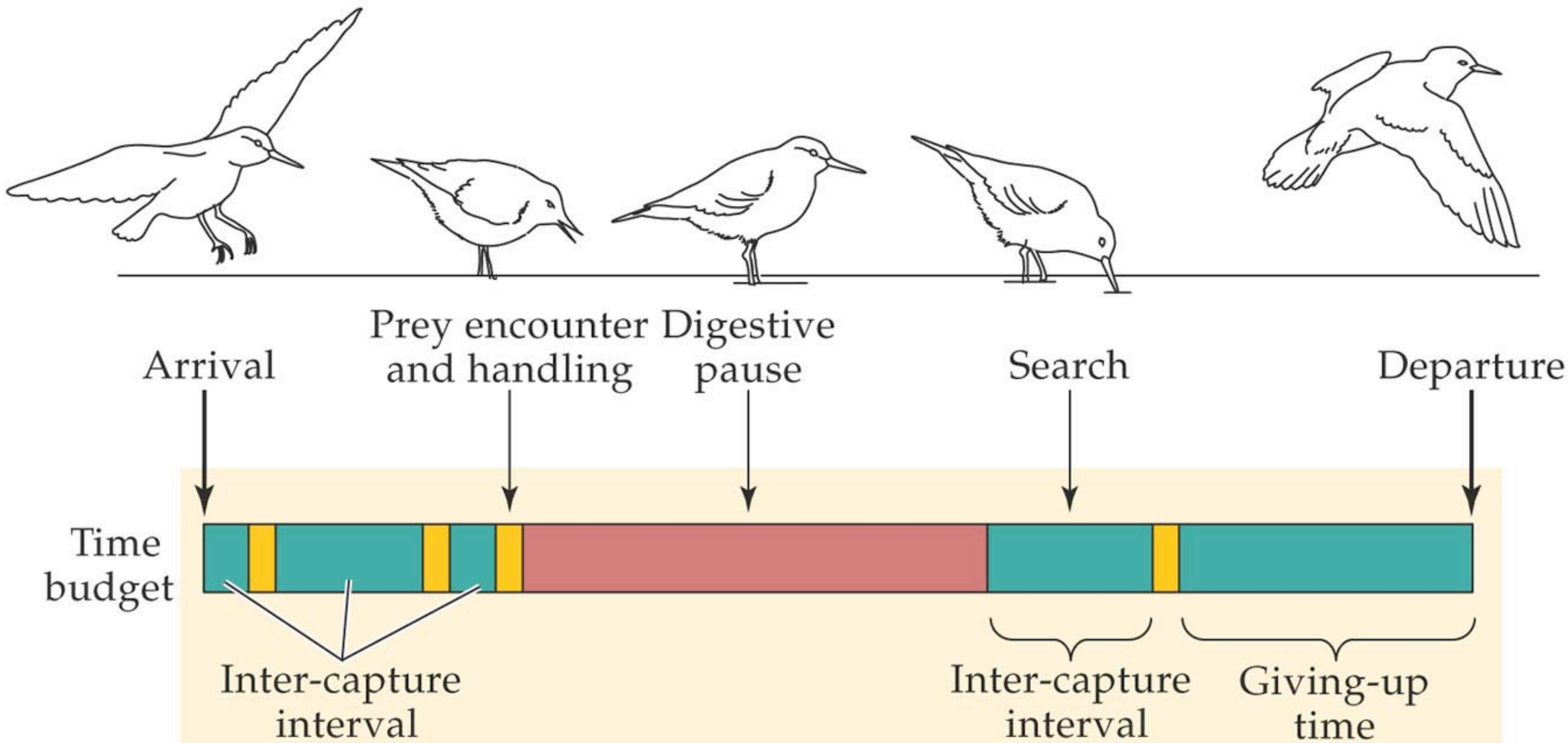
Optimal Foraging Behavior

- Extreme version of adaptationist approach
- Optimal Research Program
  - Adaptationist approach that assumes perfectly adapted animals to environment
  - Make very testable and explicit predictions
  - Controversial but rather successful

Optimal Foraging Design Hypothesis

- Based on energy intake as a currency of fitness.
  - Fitness ↑ as energy intake ↑.
- So, expect that animals will be maximally efficient foragers.
  - Maximize rate of energy intake

7.5 A foraging bout by the red



Decisions, Decisions, Decisions

- Where to feed
- What to eat
- When to feed
- How to feed
  - How to handle prey
  - How long to stay in a patch of food

Scenario: The Northwestern Crow

Feed on shellfish (Whelks)

They drop them on rocky beaches to smash open.

Only Whelks larger than 4 cm are dropped, typically from about 5 m.

Will repeat this until it breaks

Crows feeding on whelks (marine snails) fly up and drop the whelks on rocks to break them.

Height from which a shell is dropped affects its probability of breaking.

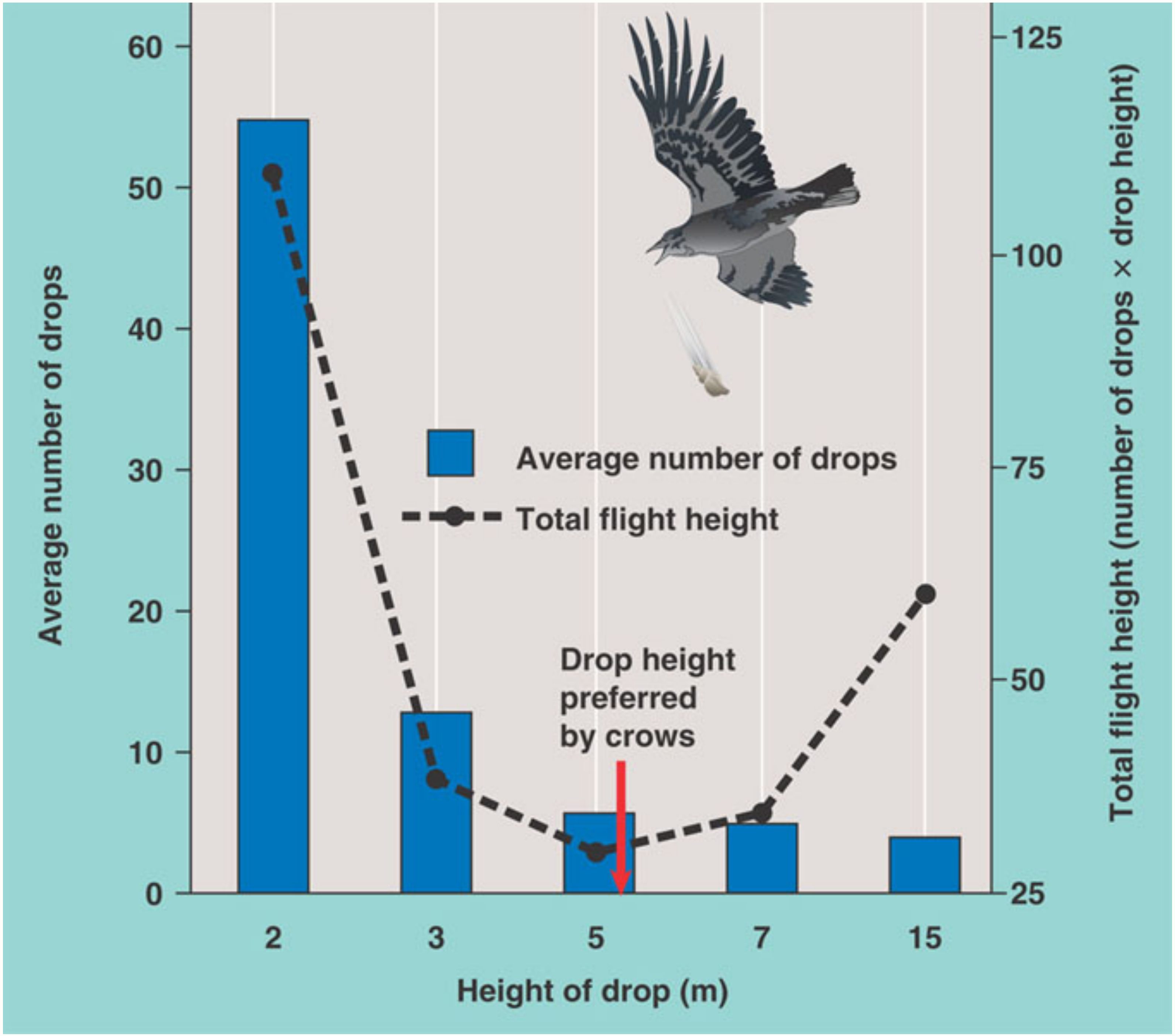
Dropping from greater height increases probability of breaking shell, but it costs energy to fly up.

Reto Zach studied crows and predicted they would fly to a height that, on average, provided the most food relative to the energy needed to break the shell.

Zach dropped shells from different heights and for each height determined the average number of drops needed to break a shell.

Then he calculated **total flight height** (number of drops x height of each flight) as a measure of the energy needed to break a shell.

Zach predicted a height of 5m would be the optimal flight height. Observed height crows flew to was 5.23, a close match.



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

Suggested Predictions

Larger whelks are more likely to break

True

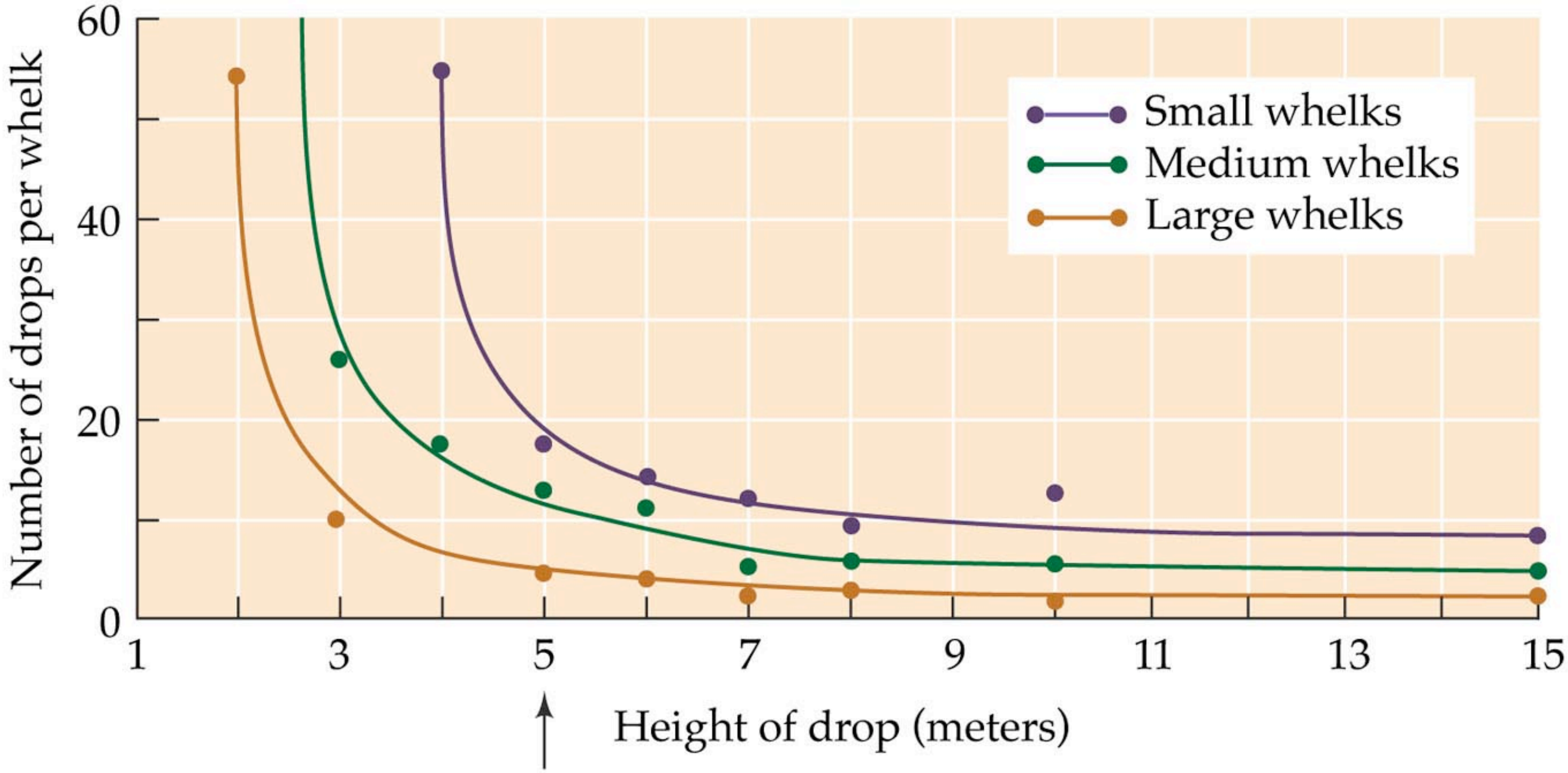
Greater than 5 m height yields a small additional probability of breaking.

True

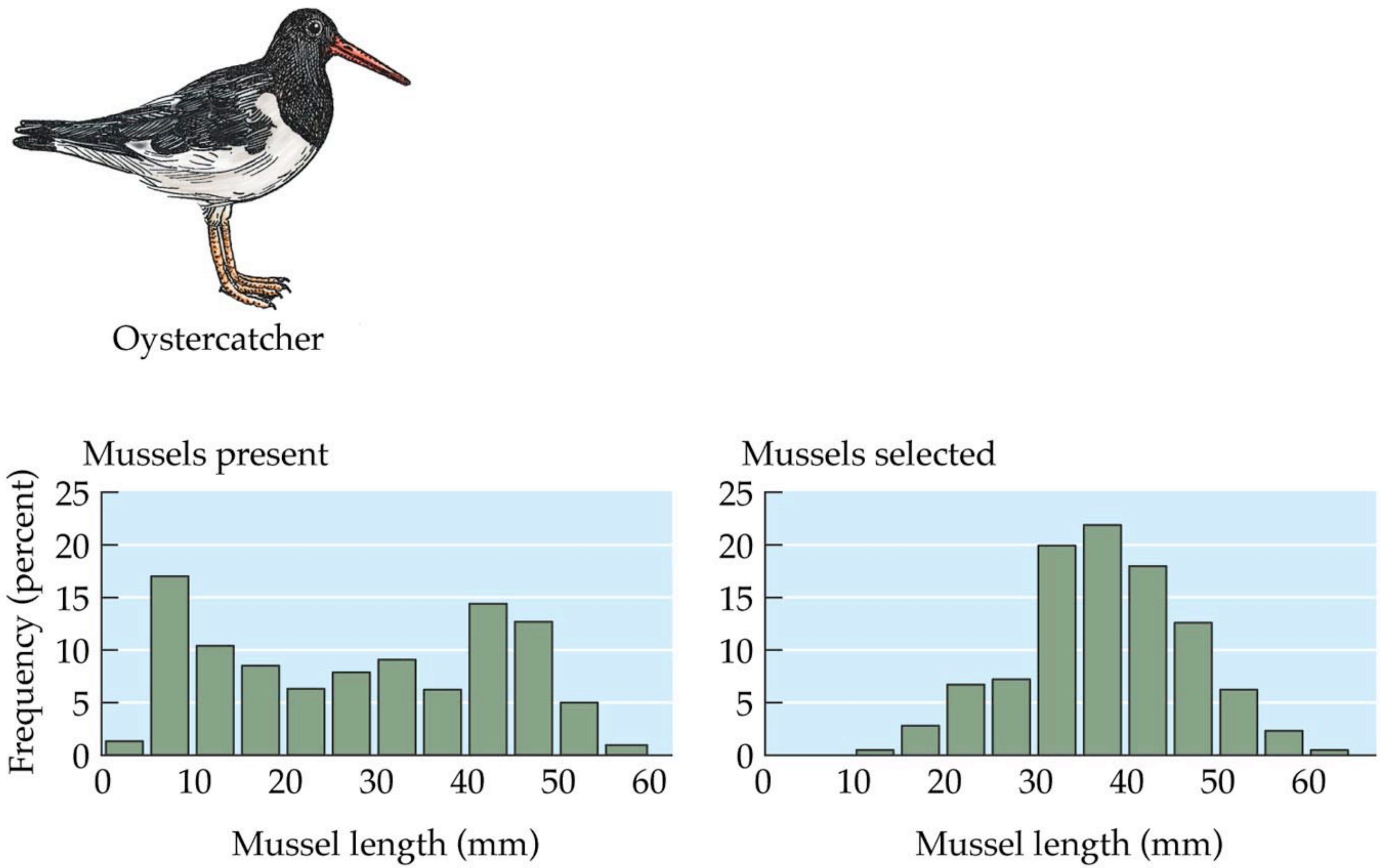
Probability of breaking is constant or increased over time

True

7.1 Optimal foraging decisions by

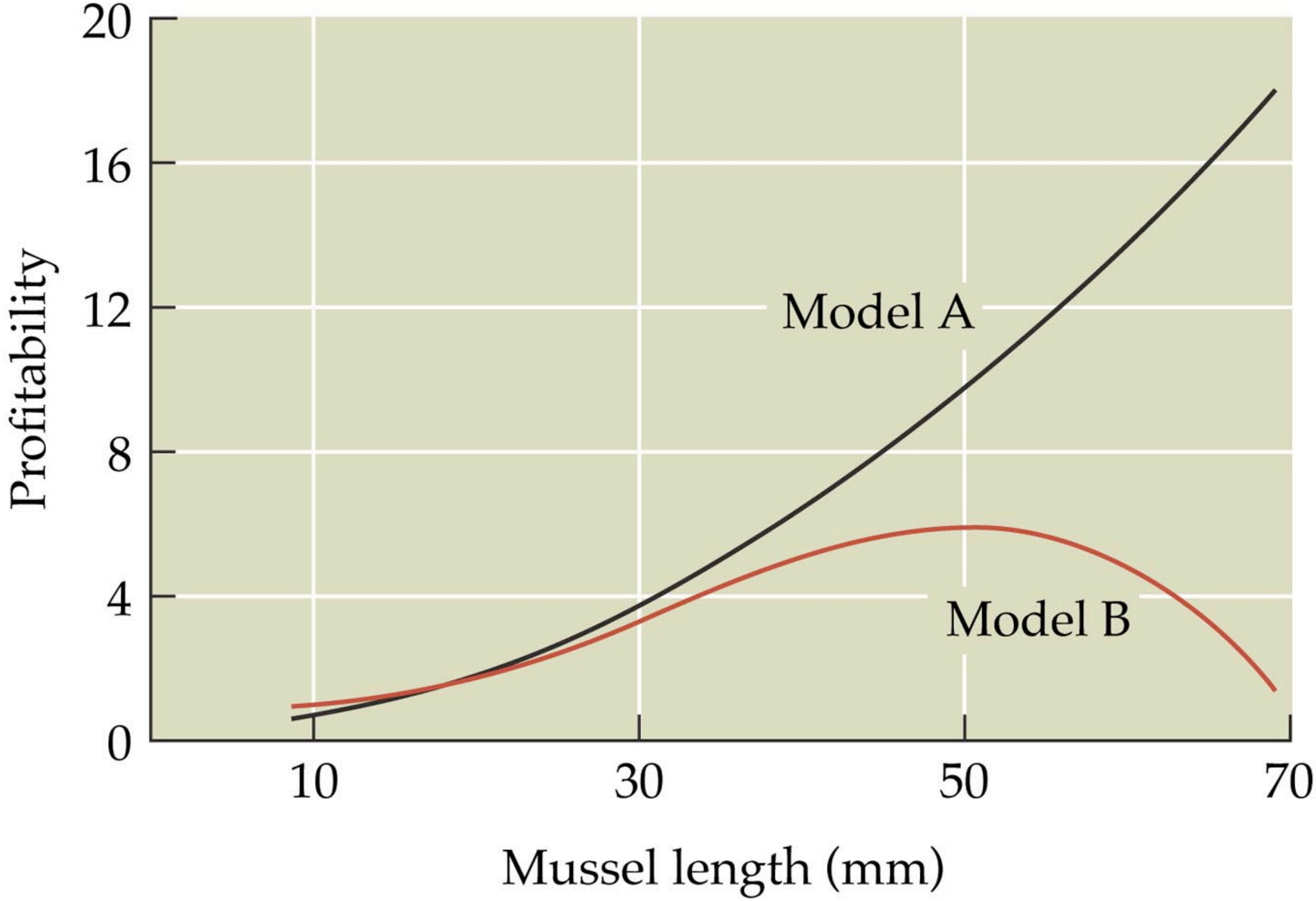


7.2 Available prey versus prey

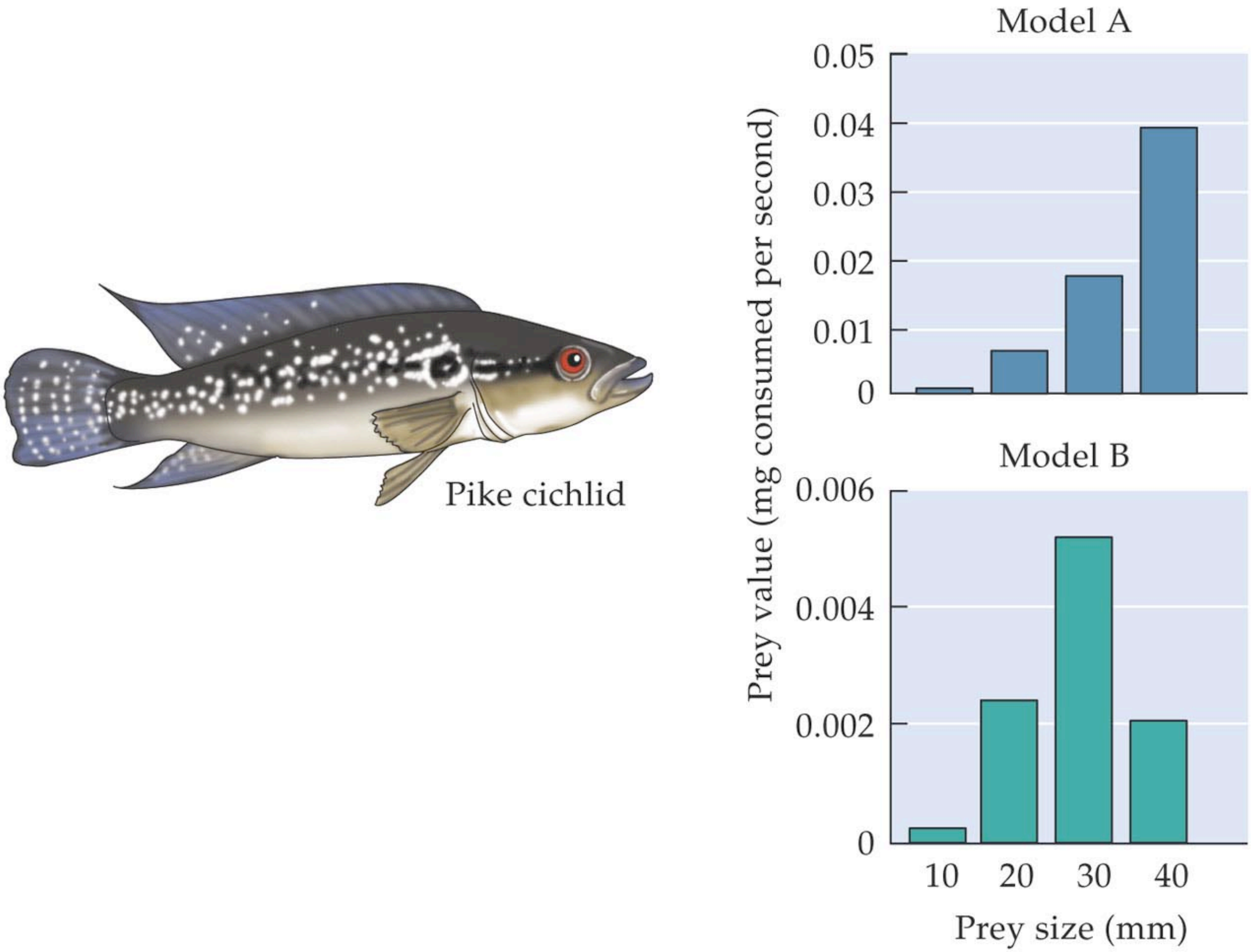


ANIMAL BEHAVIOR, Eighth Edition, **Figure 7.2**

7.3 Two optimal foraging models



7.4 Two optimal foraging models



Non-energetic Considerations

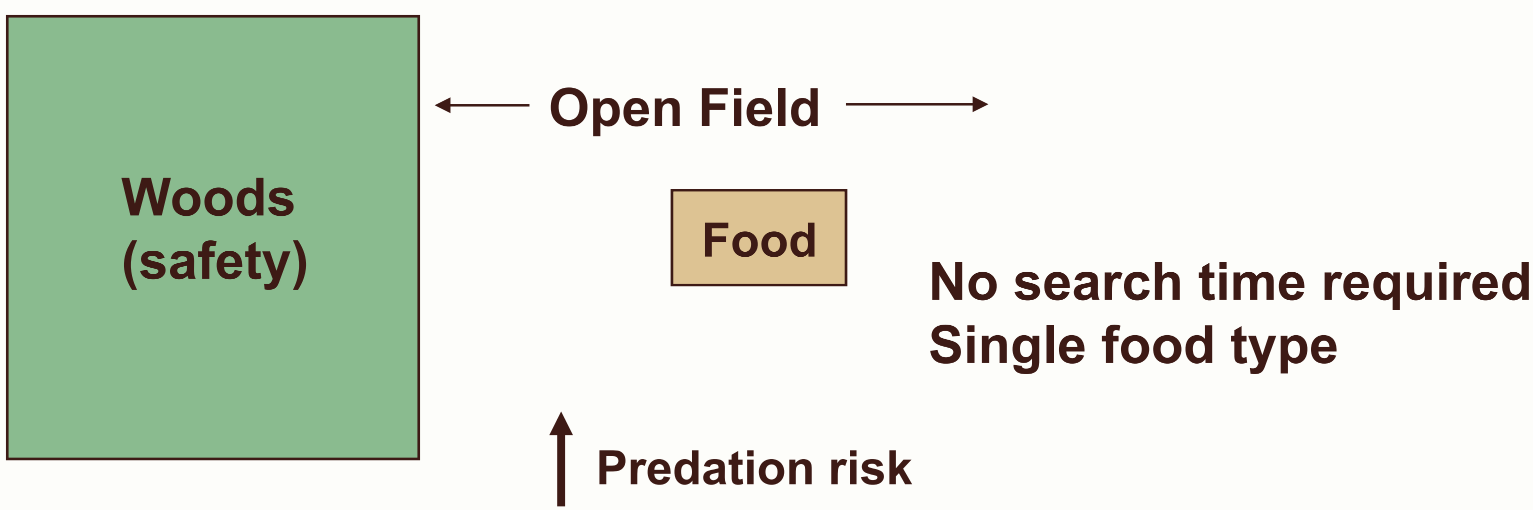
So far – selection produces animals that maximize energy intake rate

But… in many circumstances, behaviors that maximize energy intake rate will lead to a higher risk of death.

Design Hypothesis

Animals trade off energy and risk of predation to maximize survival (fitness)

Ex. with Chickadees



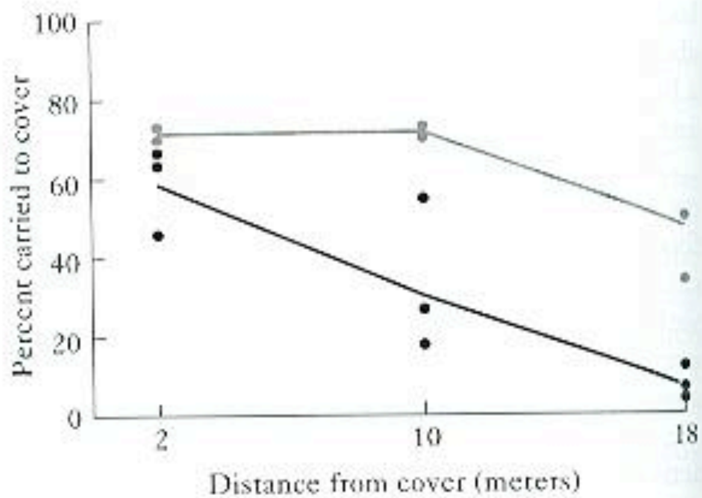
Maximize energy rate

- Stay out in patch and eat

Minimum risk of predation

- Carry each food item to woods for consumption
- Lowest energy intake rate

33 Predation risk and consumption decisions by chickadees. After a simulated hawk has passed near chickadees (grey circles), they are more likely to carry seeds from an exposed feeding site to cover before preparing and eating them than when no "predator" is present (black circles). *Source: Lima [719].*



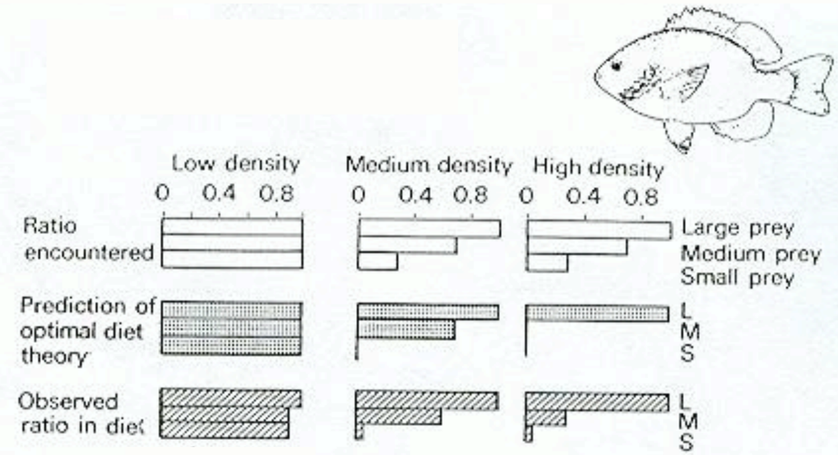
Conclusions of Chickadee Foraging

- Never see 100% carried to cover
- Never stays in open the whole time
  - Farther from cover, stay in open field more
- More costly to carry back to cover when handling time is small
  - If time to carry is greater than time to eat, then stay in the open
- Only happens if handling > round trip travel time

Examples of Non-Optimal Foraging?

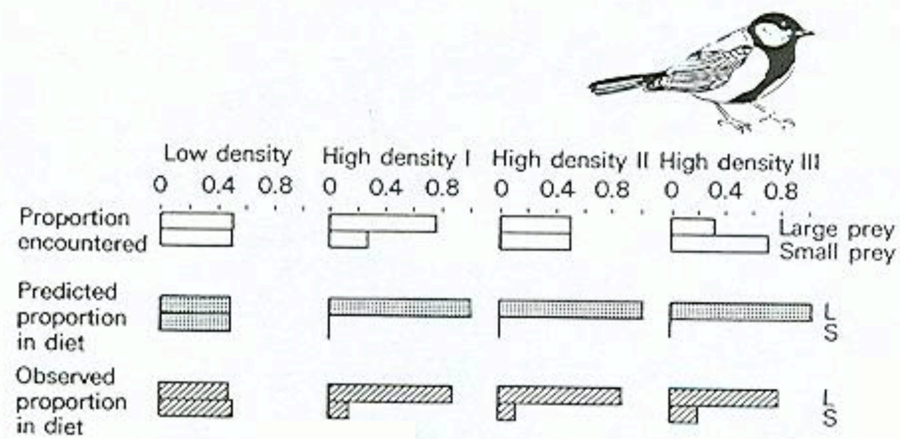
Blue gill sunfish

- Still eat small and medium prey when OFT predicts otherwise

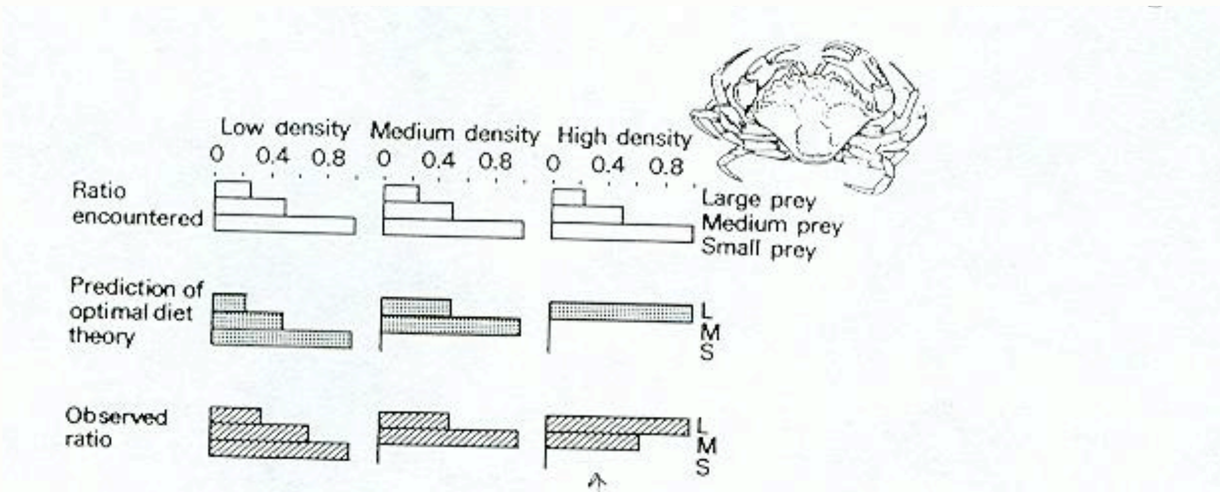


American Redstart

- Continues to make mistakes and take small prey



And More Examples



Theory does not always work

Discovery -Break claws while handling large mussels – take medium prey