7

Life History Analyses

7 Life History Analyses

- *Case Study*: Nemo Grows Up
- Life History Diversity
- Life History Continua
- Trade-Offs
- Life Cycle Evolution
- Case Study Revisited
- *Connections in Nature*: Territoriality, Competition, and Life History

All organisms produce offspring, but the number and size of offspring vary greatly.

Figure 7.1 Offspring Vary in Size and Number

Case Study: Nemo Grows Up

Figure 7.2 Life in a Sea Anemone

“Nemo” the clownfish is depicted as having a very human-like family in the movie *Finding Nemo*.

Case Study: Nemo Grows Up

In real life, 2 to 6 clownfish spend their entire adult lives within one sea anemone, but are not usually related.

The largest fish is a female; the next largest is the breeding male. The remaining fish are nonbreeding males.

Case Study: Nemo Grows Up

If the female dies, the breeding male becomes a female, and the next largest male becomes the breeding male.

There is a strict pecking order in the group, based on body size.

Case Study: Nemo Grows Up

The breeding male cares for the eggs until they hatch.

The hatchlings move away from the reef, then return as juveniles and find an anemone to inhabit.

The resident fish allow a new fish to remain only if there is room.

Introduction

An organism’s **life history** is a record of events relating to its growth, development, reproduction, and survival.

Characteristics that define the life history of a organism:

- Age and size at sexual maturity.
- Amount and timing of reproduction.
- Survival and mortality rates.

Concept 7.1: Life history patterns vary within and among species.

Individuals within a species show variation in life history traits.

The differences may be due to genetic variation or environmental conditions.

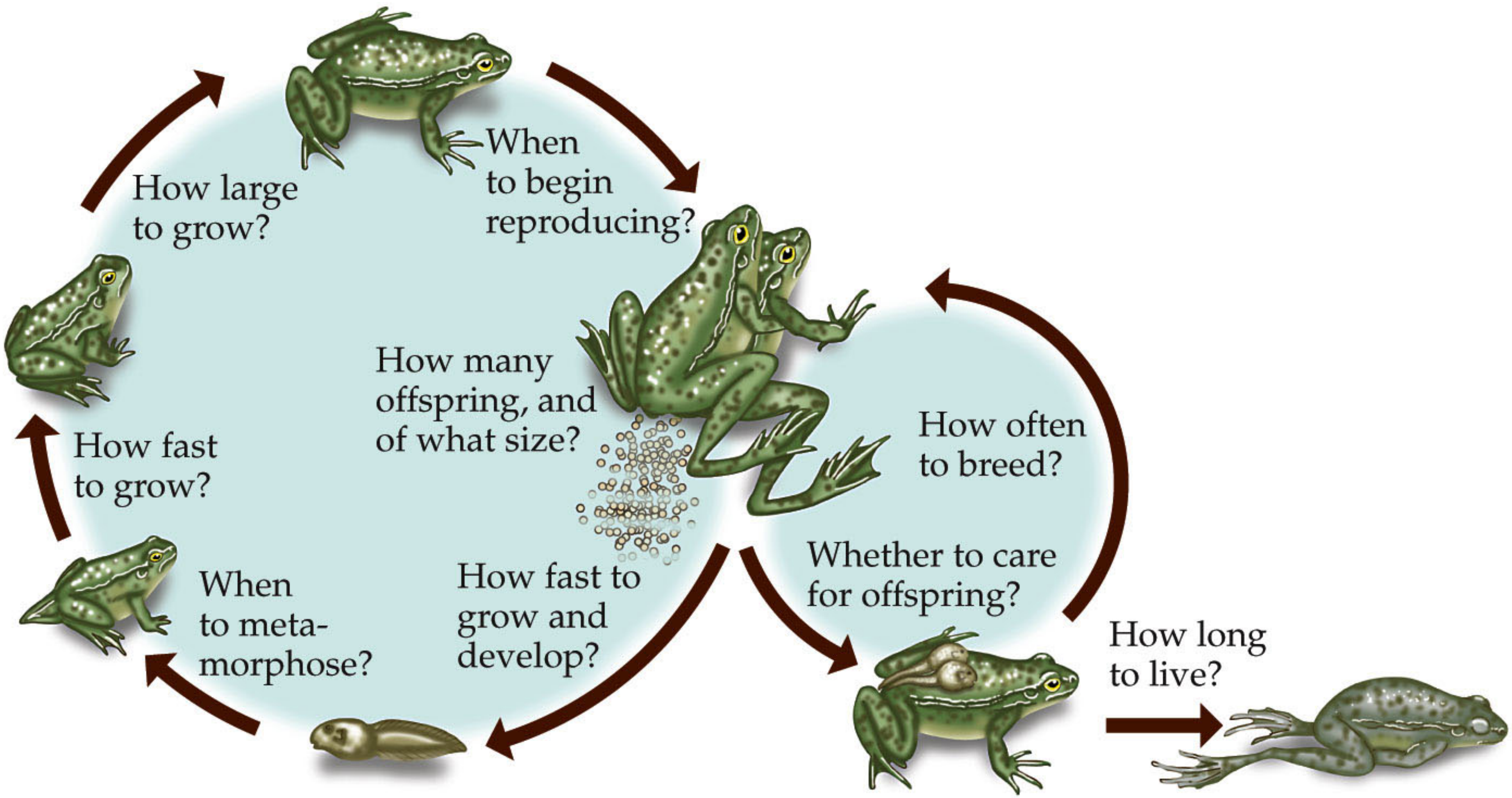
Generalizations about life history traits of a species can still be made.

Life History Diversity

The **life history strategy** of a species is the overall pattern in the average timing and nature of life history events.

It is determined by the way the organism divides its time and energy between growth, reproduction, and survival.

Figure 7.3 Life History Strategy



ECOLOGY, Figure 7.3

Life History Diversity

Life history traits influenced by genetic variation are usually more similar within families than between them.

Natural selection favors individuals whose life history traits result in their having a better chance of surviving and reproducing.

How and why have particular life history patterns evolved?

The theoretical ideal: Life histories are optimal (maximization of fitness).

Life history strategies are not necessarily perfectly adapted to maximize fitness, particularly when environmental conditions change.

Phenotypic plasticity: One genotype may produce different phenotypes under different environmental conditions.

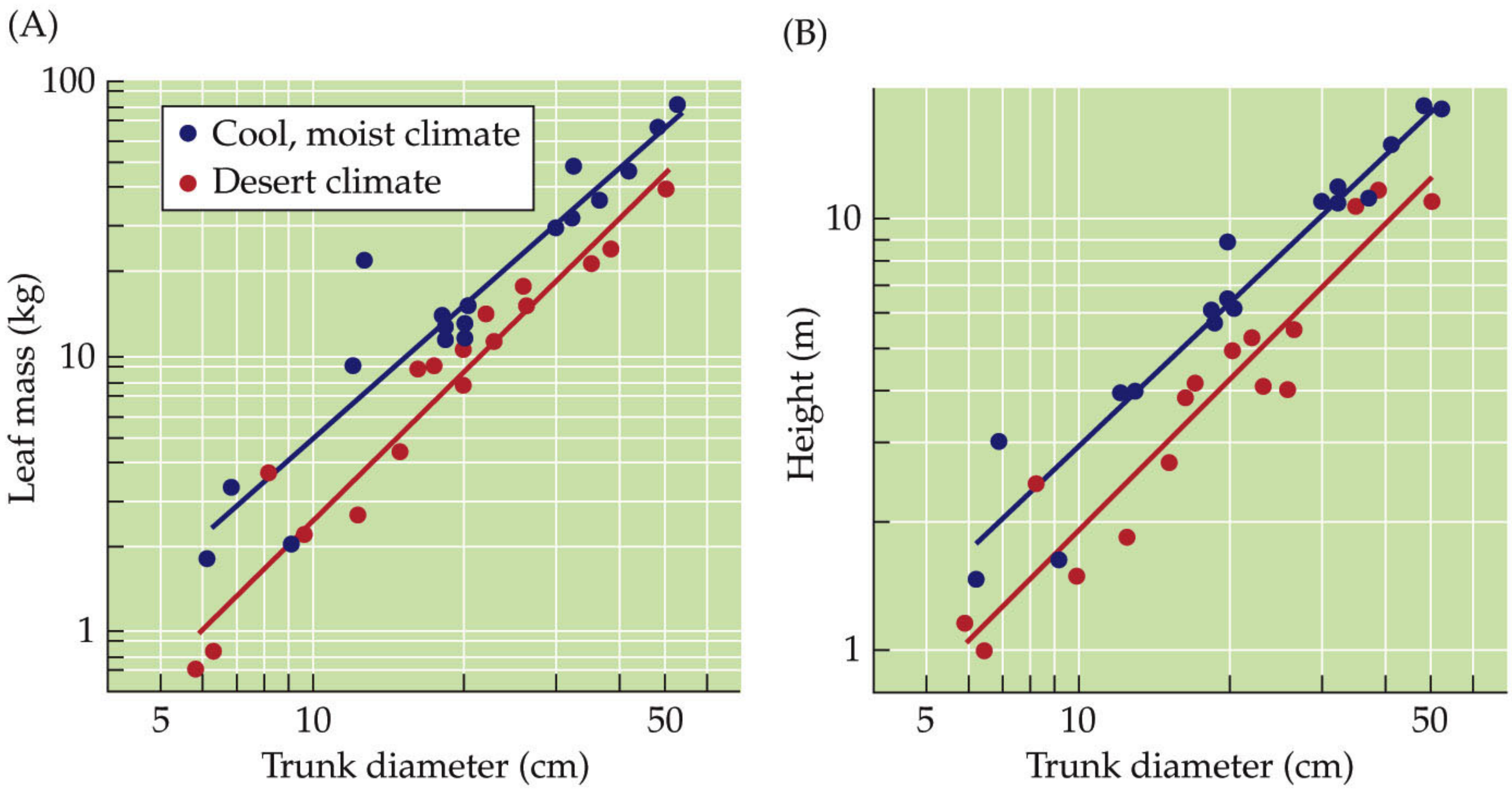
For example, growth and development may be faster in higher temperatures.

Life History Diversity

Plasticity in life history traits can be a source of plasticity in other traits.

Callaway et al. (1994) showed that ponderosa pines grown in cool, moist climates allocate more biomass to leaf growth relative to sapwood production than do those in warmer desert climates, resulting in different tree shapes.

Figure 7.4 Plasticity of Growth Form in Ponderosa Pines



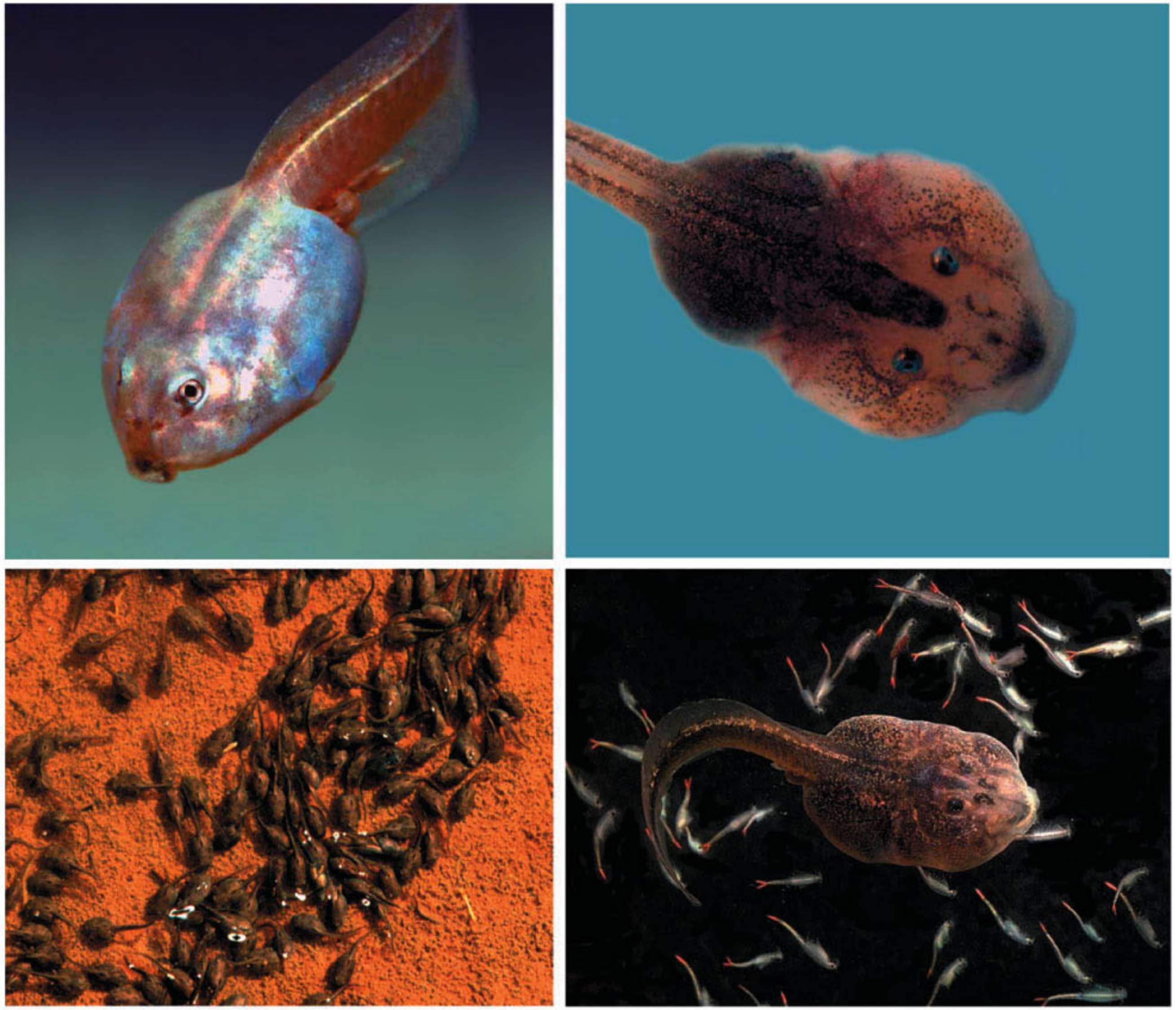
Phenotypic plasticity may produce a continuous range of growth rates; or discrete types—**morphs**.

Polyphenism—a single genotype produces several distinct morphs.

Spadefoot toad tadpoles in Arizona ponds contain both omnivore morphs and larger carnivore morphs.

Figure 7.5 Polyphenism in Spadefoot Toad Tadpoles

(A) Omnivore morph | (B) Carnivore morph



(A) Omnivores feed on the pond bottom on detritus

(B) Carnivores feed in the water column on fairy shrimp

Life History Diversity

Carnivore tadpoles grow faster and metamorphose earlier. They are favored in ephemeral ponds that dry up quickly.

The omnivores grow more slowly and are favored in ponds that persist longer, because they metamorphose in better conditions and have better chances of survival as juveniles.

The different body shapes result from differences in the relative growth rates of different body parts: Carnivores have bigger mouths and stronger jaw muscles because of accelerated growth in those areas.

Allometry: Different body parts grow at different rates, resulting in differences in shape or proportion.

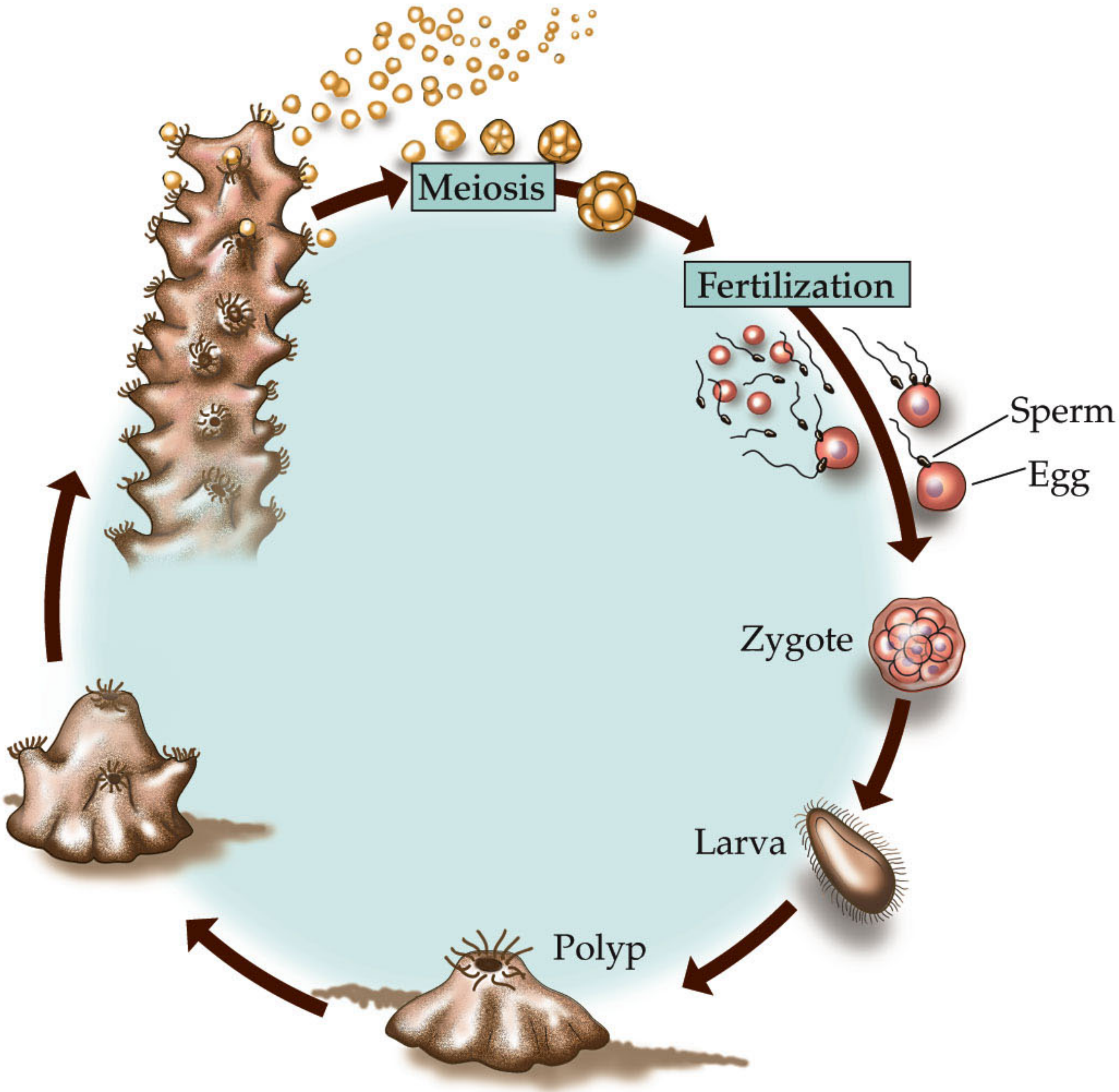
Phenotypic plasticity may be adaptive in many cases, but adaptation must be demonstrated rather than assumed.

Organisms have evolved many different modes of reproduction.

Asexual reproduction: Simple cell division—all prokaryotes and many protists.

Some multicellular organisms reproduce both sexually and asexually (e.g., corals).

Figure 7.6 Life Cycle of a Coral



Sexual reproduction has benefits: Recombination promotes genetic variation; may provide protection against disease.

And disadvantages: An individual transmits only half of its genome to the next generation; growth rate of populations is slower.

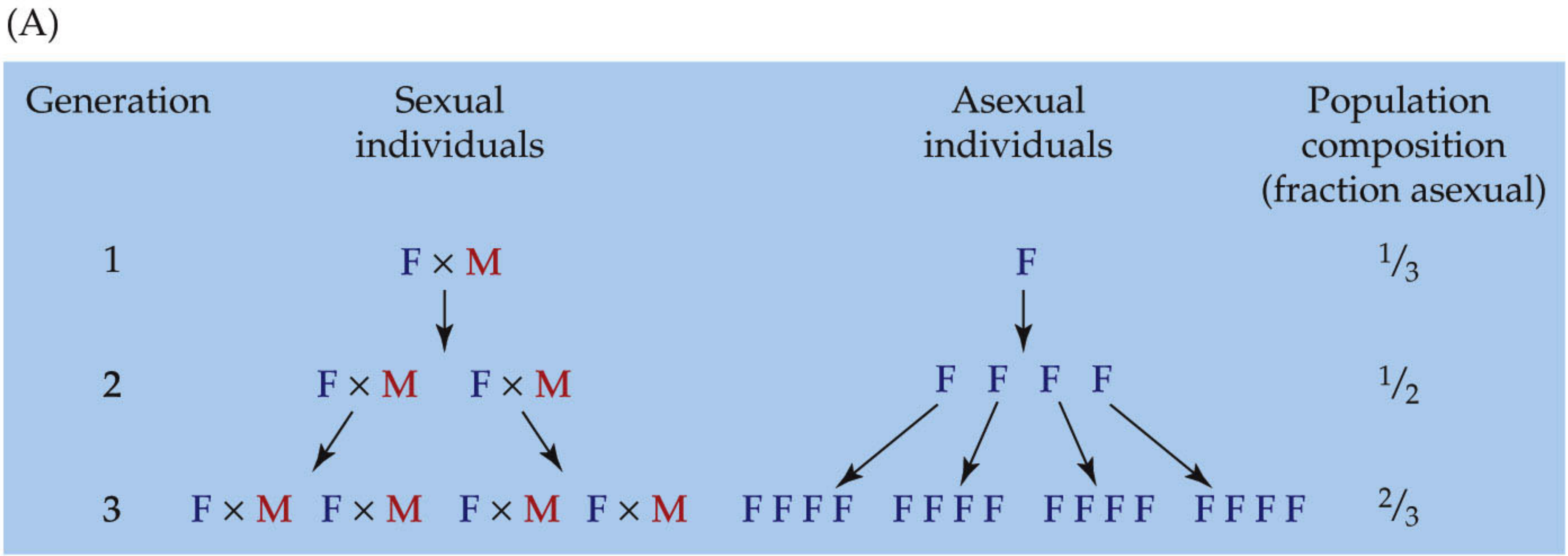
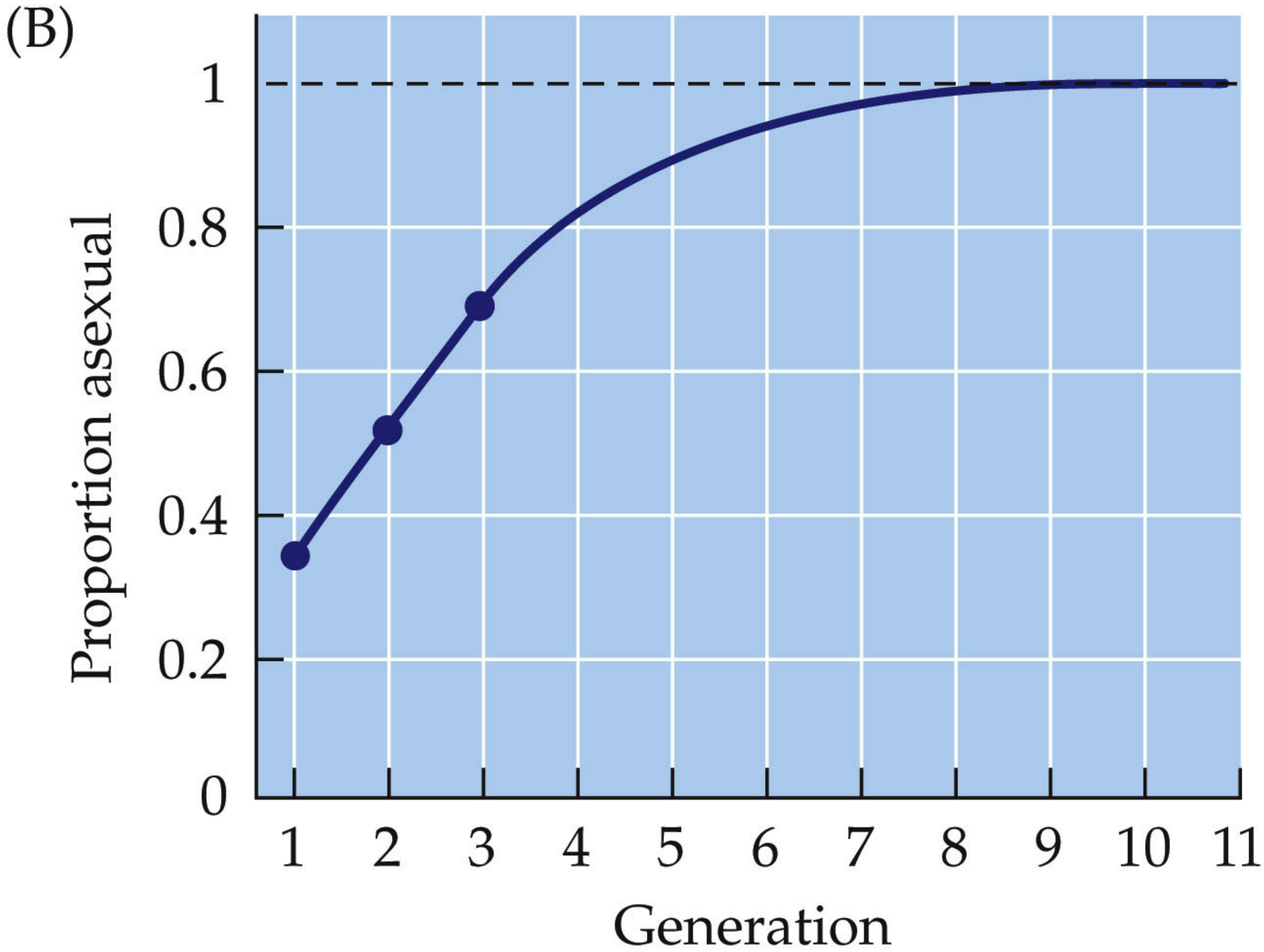

(A)
Generation
Sexual individuals
Asexual individuals
Population composition (fraction asexual)
1
F × M
F
1/3
2
F × M F × M
F F F F
1/2
3
F × M F × M F × M F × M
F F F F F F F F F F F F F F F F
2/3

Figure 7.7 The Cost of Sex (Part 2)



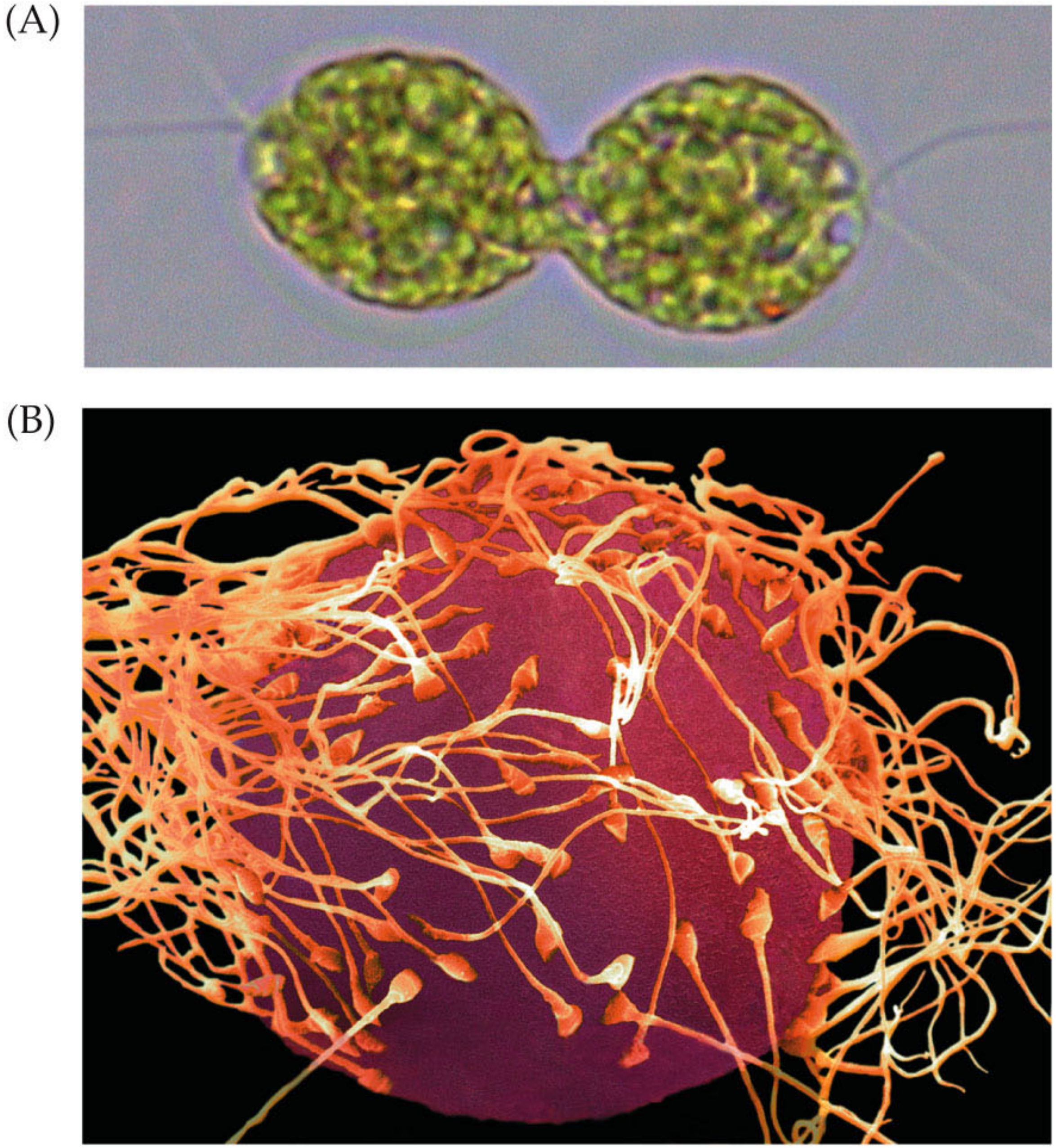
ECOLOGY, Figure 7.7 (Part 2)

Isogamy: When gametes are of equal size.

Organisms such as the green alga *Chlamydomonas reinhardii* have two *mating types* that produce isogametes.

Anisogamy: Gametes of different sizes. Usually the egg is much larger and contains more nutritional material.

Most multicellular organism produce anisogametes.


(A)
(B)

Complex life cycles involve at least two distinct stages that may have different body forms and live in different habitats.

Transition between stages may be abrupt.

Metamorphosis: Abrupt transition in form from the larval to the juvenile stage.

Life History Diversity

Most vertebrates have simple life cycles without abrupt transitions.

But complex life cycles are common in animals, including insects, marine invertebrates, amphibians, and some fishes.

Why complex life cycles?

Small offspring may experience the environment very differently than the larger parents.

For example, a tadpole is more strongly affected by surface tension and viscosity than an adult frog.

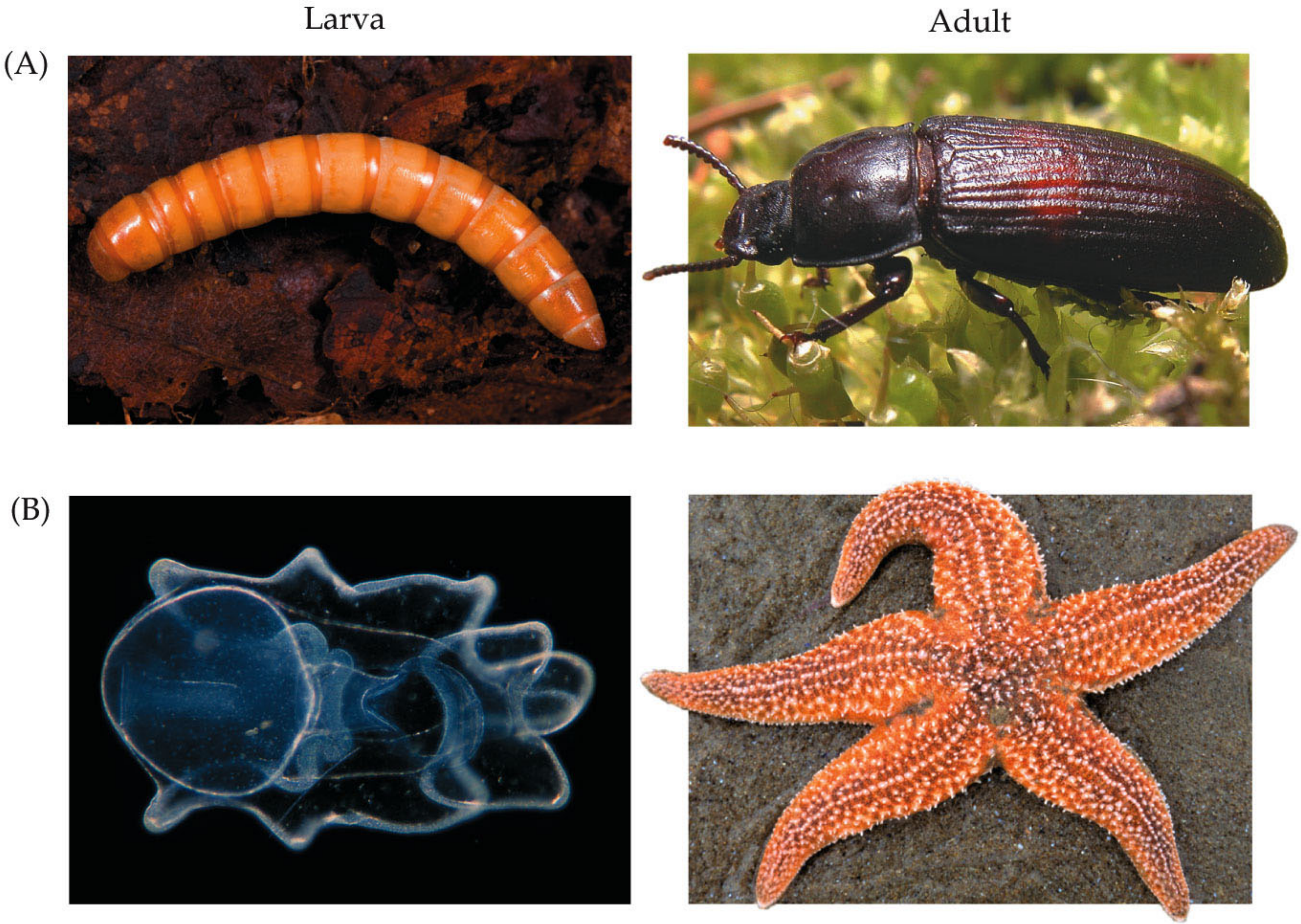
Parents and offspring can be subject to different selection pressures.

Life History Diversity

About 80% of animal species undergo metamorphosis at some time in their life cycle.

Some species have lost the complex life cycle and have **direct development**—they go from fertilized egg to juvenile without passing through a larval stage.

Figure 7.9 The Pervasiveness of Complex Life Cycles

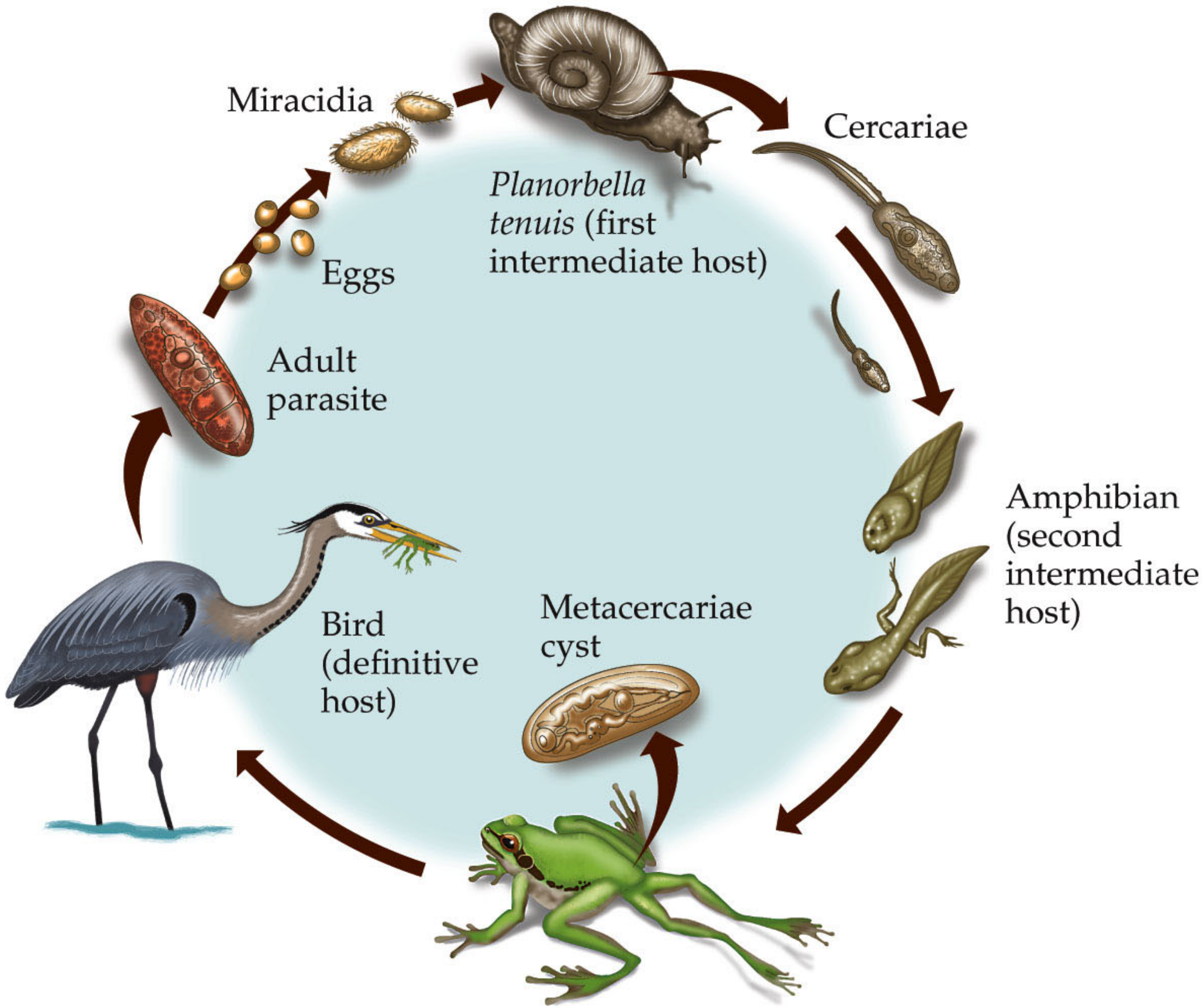


Life History Diversity

Many parasites have evolved complex life cycles with one or more specialized stages for each host.

For example, the parasite *Ribeiroia* has three specialized stages.

Figure 1.3 The Life Cycle of *Ribeiroia*

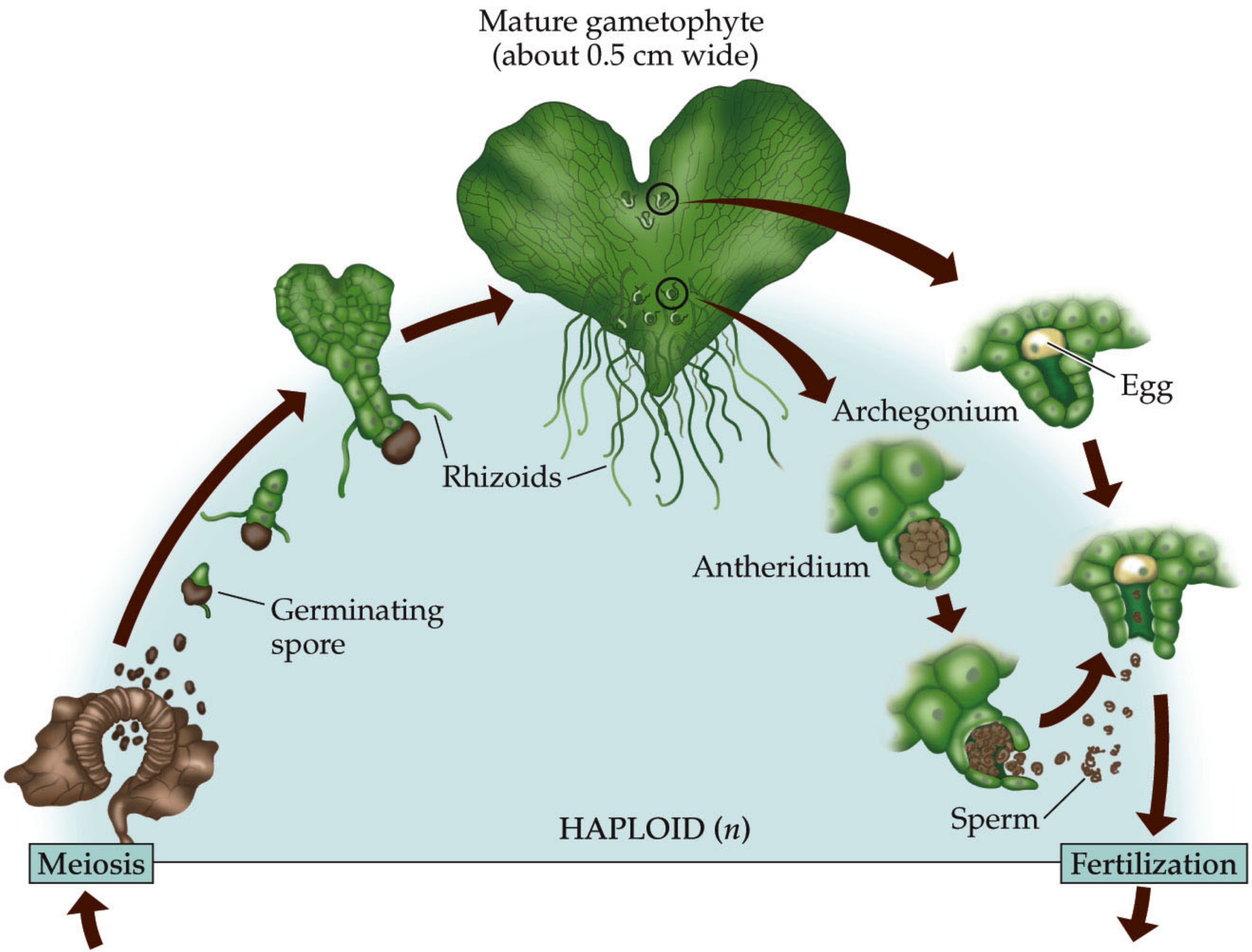


Life History Diversity

Many plants, algae, and protists also have complex life cycles.

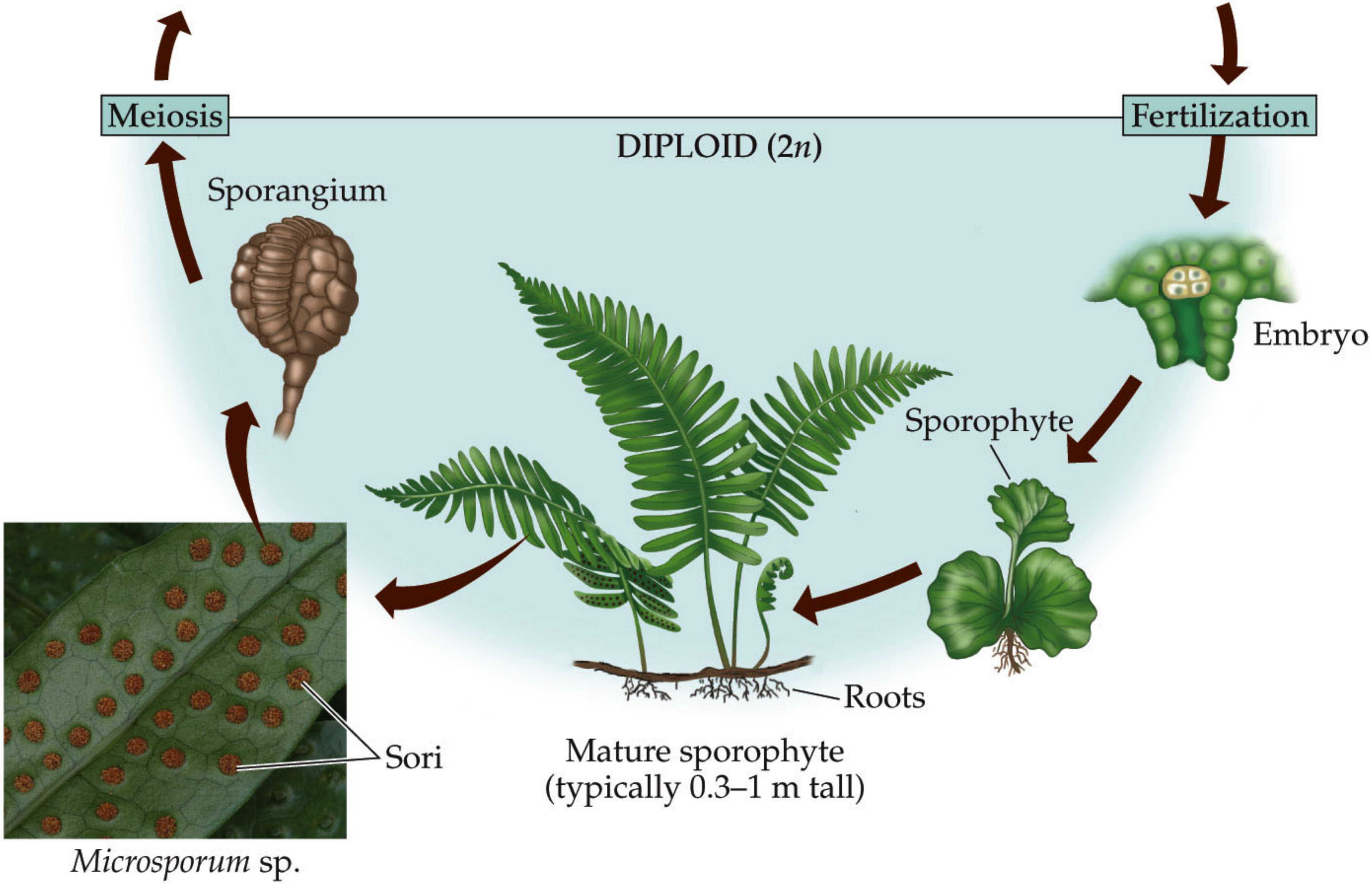
Plants and most algae have **alternation of generations** in which a multicellular diploid **sporophyte** alternates with a multicellular haploid **gametophyte**.

Figure 7.10 Alternation of Generations in a Fern (Part 1)



ECOLOGY, Figure 7.10 (Part 1)

Figure 7.10 Alternation of Generations in a Fern (Part 2)



ECOLOGY, Figure 7.10 (Part 2)

Concept 7.2: Reproductive patterns can be categorized along several continua.

Several classification schemes have been proposed to categorize the vast diversity of reproductive patterns.

The schemes place patterns on continua with extremes at each end.

Life History Continua

How many reproductive bouts occur during the organism’s lifetime?

Semelparous species reproduce only once.

Iteroparous species can reproduce multiple times.

Semelparous species include:

- Annual plants.
- *Agave*—vegetative growth can last up to 25 years. It also produces clones asexually.
- Giant Pacific octopus—a female lays a single clutch of eggs and broods them for 6 months, dying after they hatch.

Life History Continua

Iteroparous species include:

- Trees such as pines and spruces.
- Most large mammals.

***r*-selection** and ***K*-selection** describe two ends of a continuum of reproductive patterns.

r is the *intrinsic rate of increase* of a population.

r-selection is selection for high population growth rates; in uncrowded environments, newly disturbed habitats, etc.

Life History Continua

K is the carrying capacity for a population.

K-selection is selection for slower growth rates in populations that are at or near *K*; crowded conditions, efficient reproduction is favored.

Life History Continua

The *r*–*K* continuum is a spectrum of population growth rates, from fast to slow.

On the *r*-selected end: Short life spans, rapid development, early maturation, low parental investment, high rates of reproduction.

Most insects, small vertebrates such as mice, weedy plant species.

Life History Continua

On the *K*-selected end: Long-lived, develop slowly, delayed maturation, invest heavily in each offspring, and low rates of reproduction.

Large mammals, reptiles such as tortoises and crocodiles, and long-lived plants such as oak and maple trees.

Life History Continua

Most life histories are intermediate between these extremes.

Braby (2002) compared three species of Australian butterflies. The one in drier, less predictable habitats has more *r*-selected characteristics.

The two species found in more predictable wet forest habitats have *K*-selected characteristics.

Life History Continua

A classification scheme for plant life histories is based on stress and disturbance (Grime 1977).

Stress—any factor that reduces vegetative growth.

Disturbance—any process that destroys plant biomass.

Life History Continua

Four habitat types possible:

- Low stress, low disturbance.
- High stress, low disturbance.
- Low stress, high disturbance.
- High stress, high disturbance—not suitable for plant growth.

Life History Continua

Three species/habitat types:

- Low stress and low disturbance—**competitive plants** that are superior in their ability to acquire light, minerals, water, and space, have a selective advantage.

- High stress, low disturbance—**stress-tolerant** plants are favored.

Features can include phenotypic plasticity, slow rates of water and nutrient use, and low palatability to herbivores.

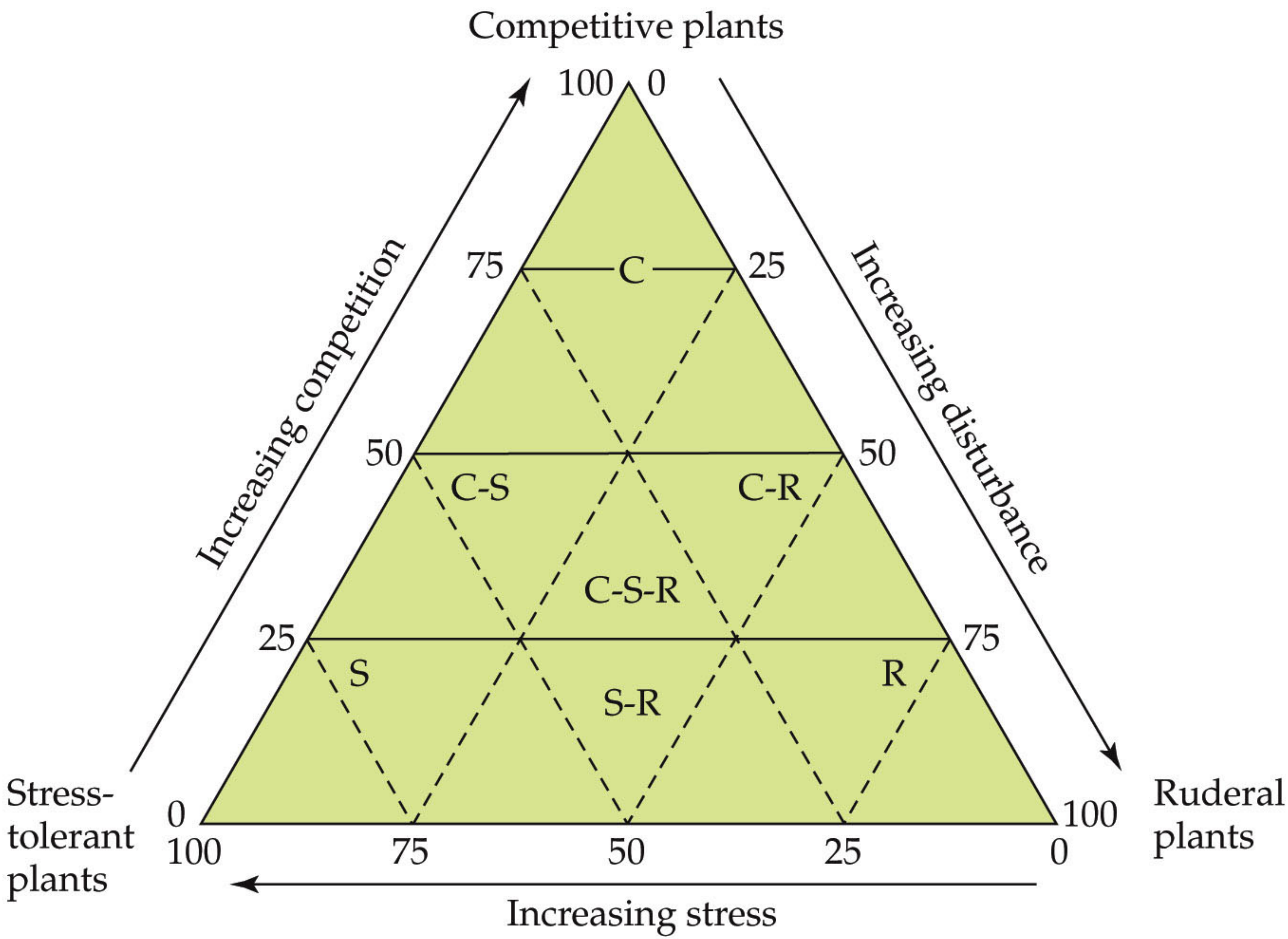
Life History Continua

- Low stress, high disturbance—**ruderal plants** dominate—short life spans, rapid growth rates, heavy investment in seed production.

Seeds can survive for long periods until conditions are right for rapid germination and growth.

Ruderal species can exploit habitats after disturbance has removed competitors.

Figure 7.12 Grime's Triangular Model



ECOLOGY, Figure 7.12

Life History Continua

Comparing to the *r*–*K* continuum:

Ruderal plants are similar to *r*-selected species; stress-tolerant plants correspond to *K*-selected species.

Competitive plants occupy the middle of the *r*–*K* continuum.

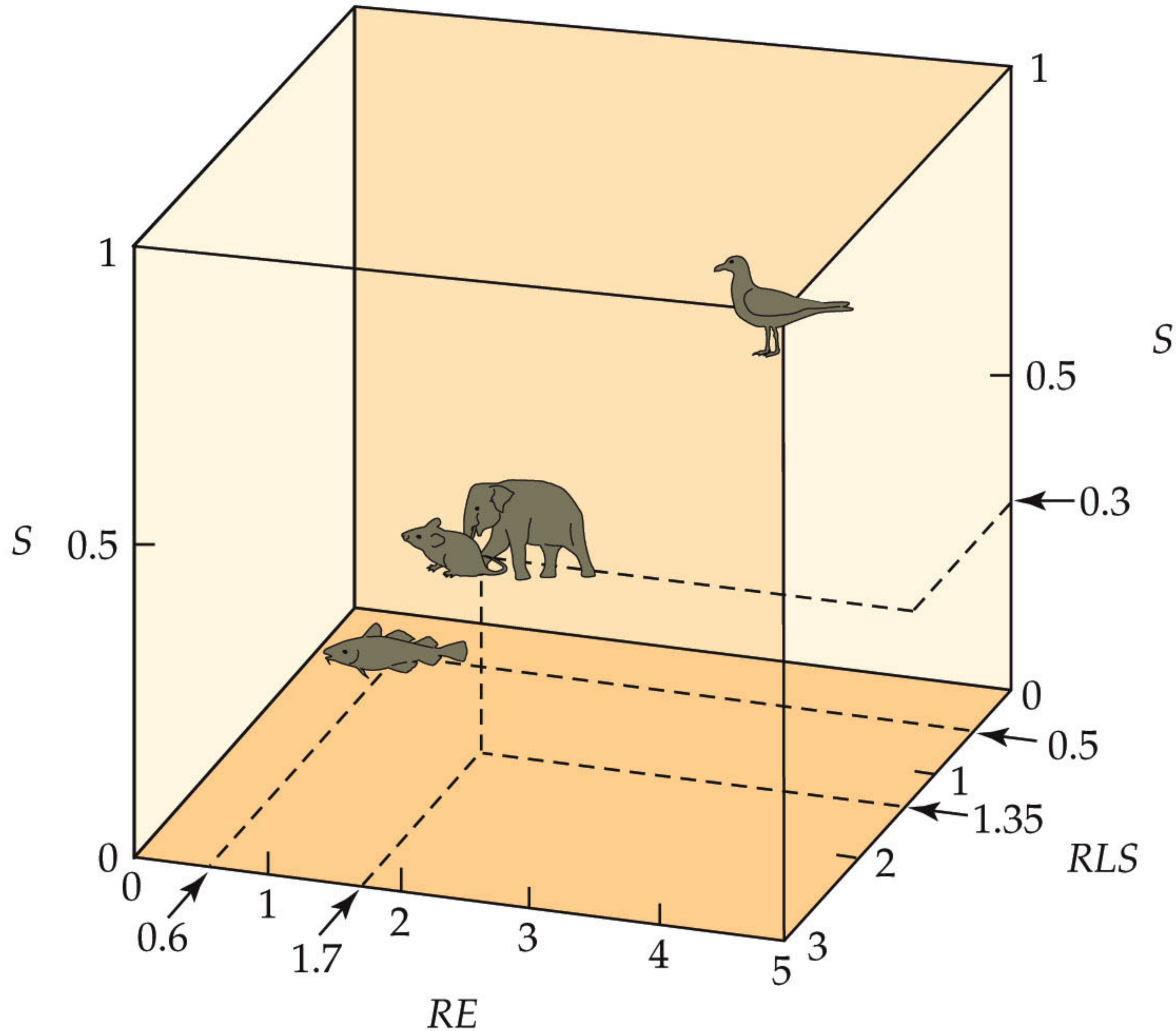
Life History Continua

A new scheme proposes a "life history cube" that removes the influence of size and time (Charnov 2002).

The cube has three dimensionless axes:

1. Size of offspring relative to adults.
2. The reproductive life span divided by the time to reach maturity.
3. Adult reproductive effort per unit of adult mortality.

Figure 7.13 Charnov's Life History Cube



ECOLOGY, Figure 7.13

Life History Continua

The third axis is a measure of **reproductive effort**: The quantity of energy and resources devoted to reproduction, corrected to take into account the costs of reproduction.

Life History Continua

Charnov’s life history cube may be most useful when comparing life histories across broad range of taxonomy or size.

Grime’s scheme may be best for comparisons between plant taxa.

The *r*–*K* continuum is useful in relating life history characteristics to population growth characteristics.

Concept 7.3: There are trade-offs between life history traits.

Trade-offs: Organisms allocate limited energy or resources to one structure or function at the expense of another.

Trade-offs shape and constrain life history evolution.

Trade-Offs

Trade-offs between size and number of offspring: The larger an organism’s investment in each individual offspring, the fewer offspring it can produce.

Investment includes energy, resources, time, and loss of chances to engage in alternative activities such as foraging.

Trade-Offs

"Lack clutch size": Maximum number of offspring a parent can successfully raise to maturity.

Named for studies by David Lack (1947): Clutch size is limited by the maximum number of offspring the parents can raise at one time.

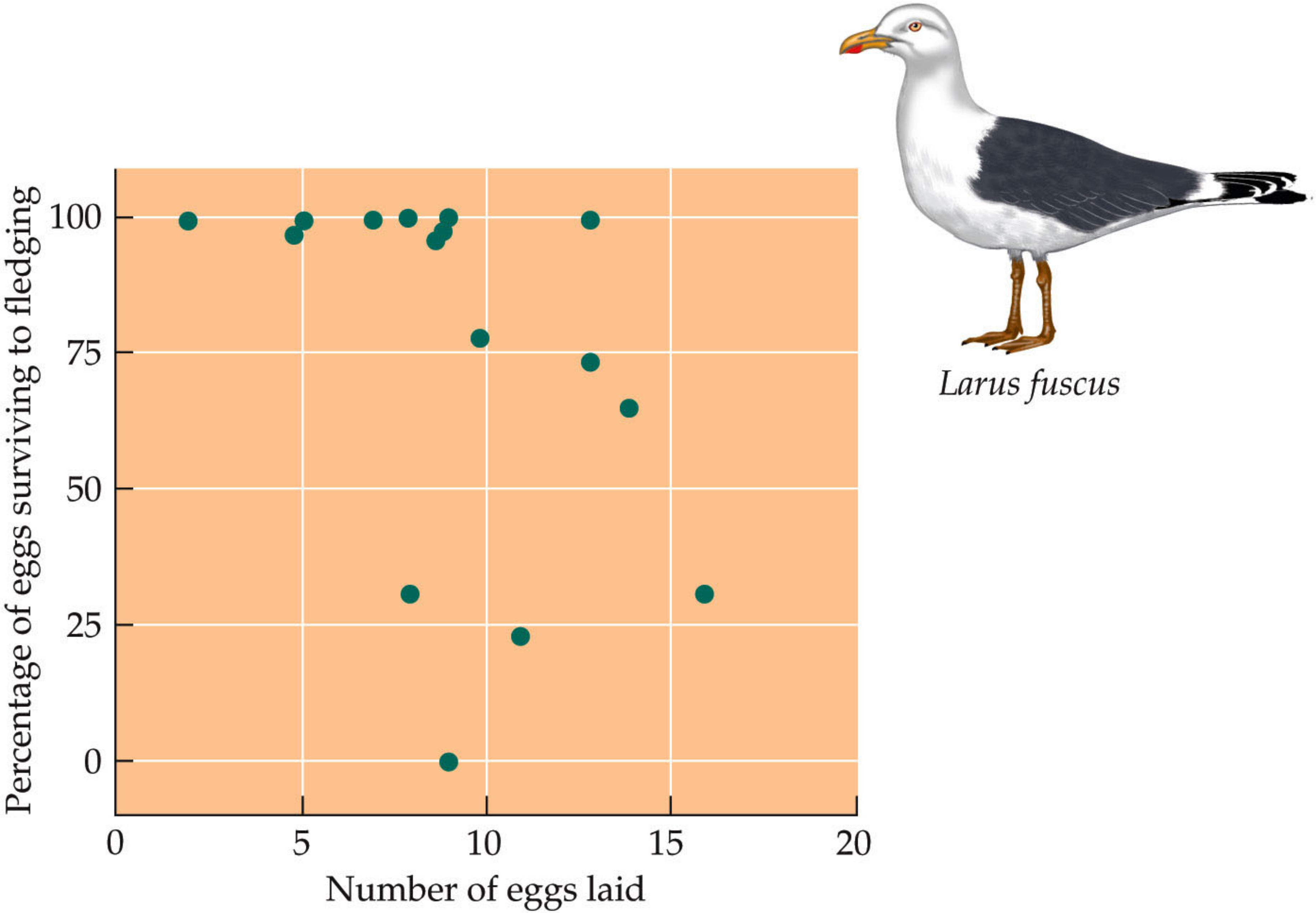
Trade-Offs

Lack noticed that clutch size increased at higher latitudes,perhaps because longer periods of daylight allowed parents more time for foraging, and they could feed greater numbers of offspring in a day.

Trade-Offs

Experimental manipulation of clutch size in lesser black-backed gulls showed that in larger clutches, offspring have less chance of survival (Nager et al. 2000).

Figure 7.14 Clutch Size and Survival



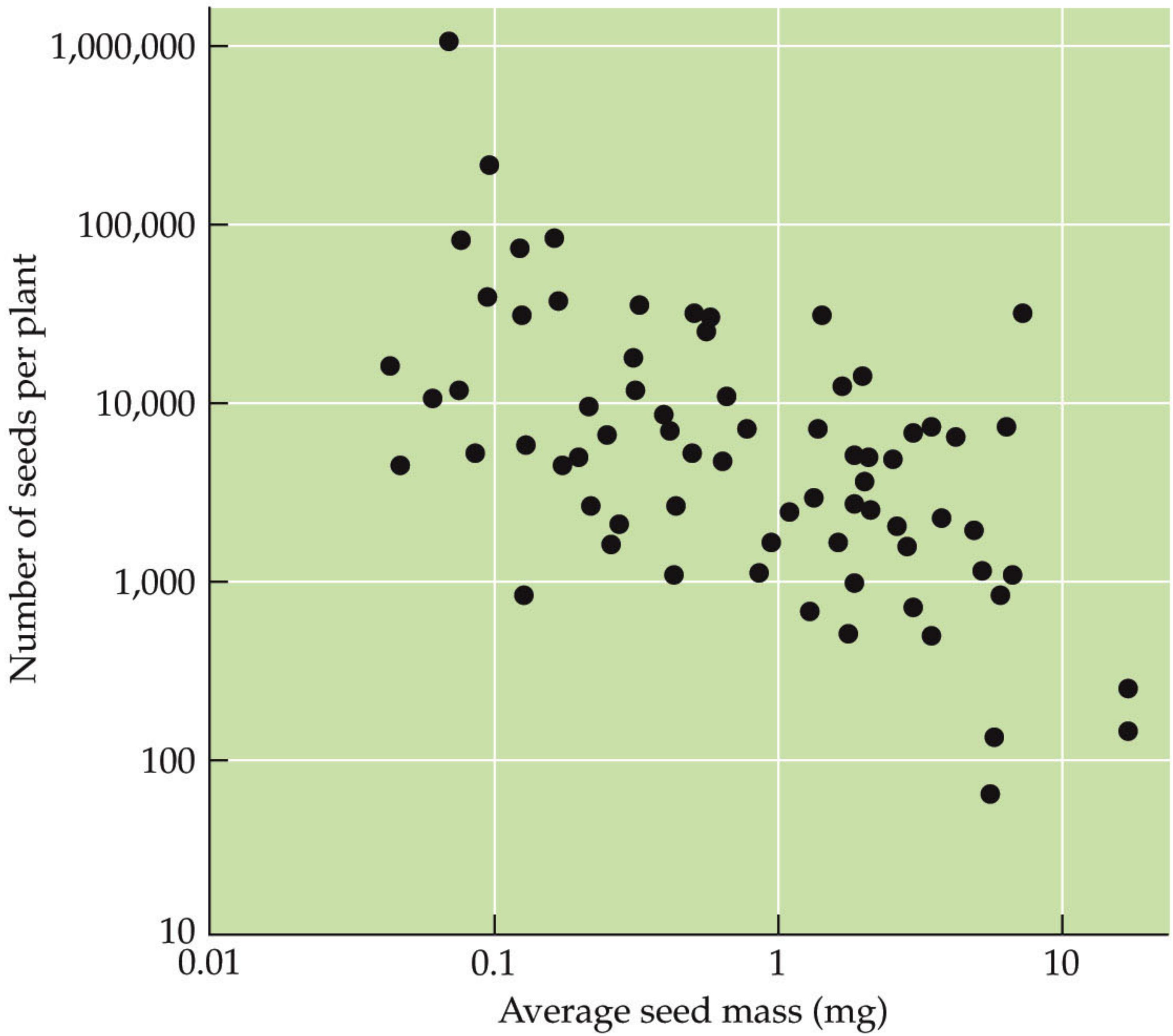
Trade-Offs

In species without parental care, reproductive investment is measured as resources invested in *propagules* (eggs or seeds).

Size of the propagule is a trade-off with the number produced.

In plants, seed size is negatively correlated with the number of seeds produced.

Figure 7.15 Seed Size–Seed Number Trade-Offs in Plants



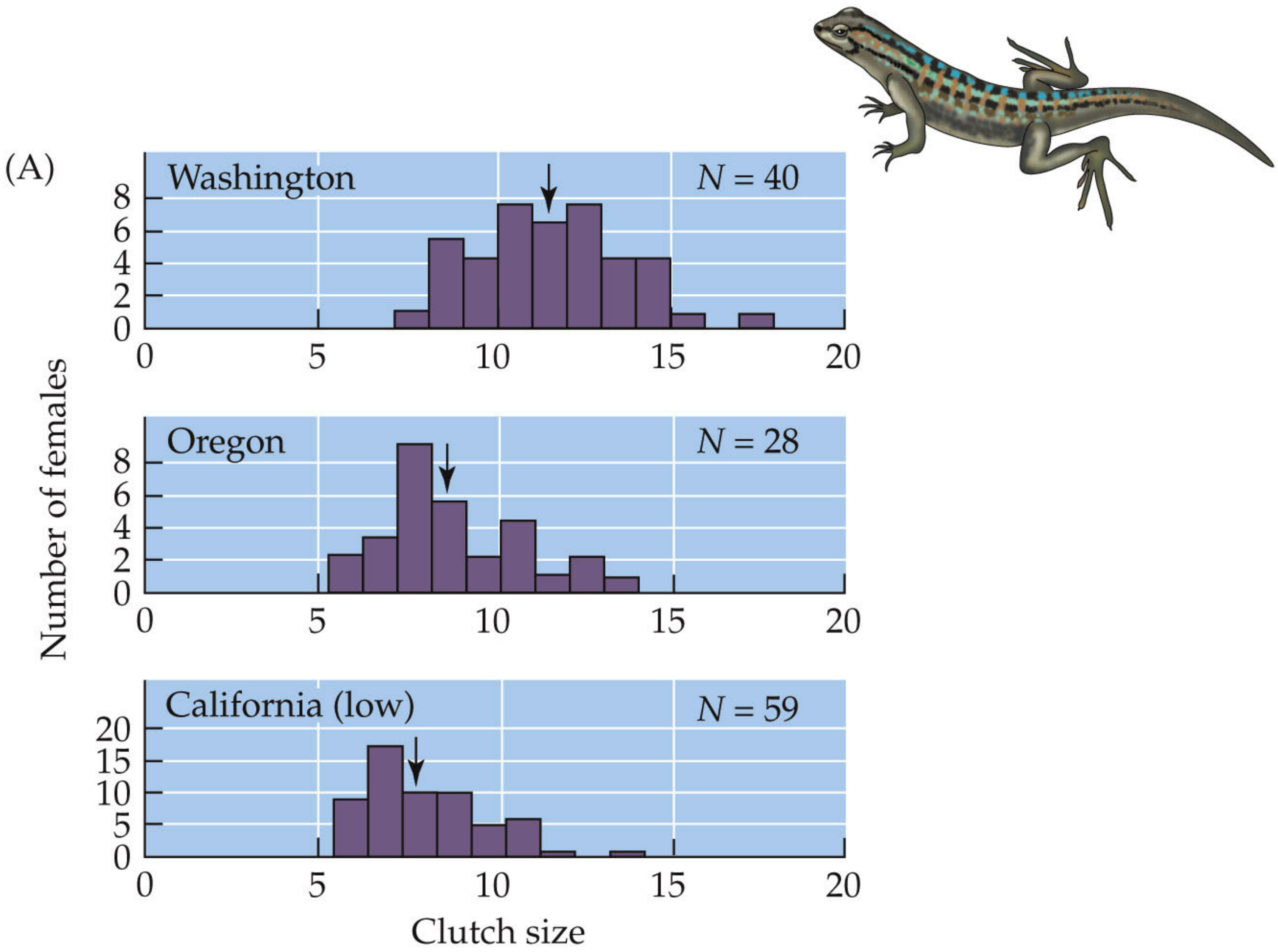
ECOLOGY, Figure 7.15

Trade-Offs

The size–number trade-off can also occur within species.

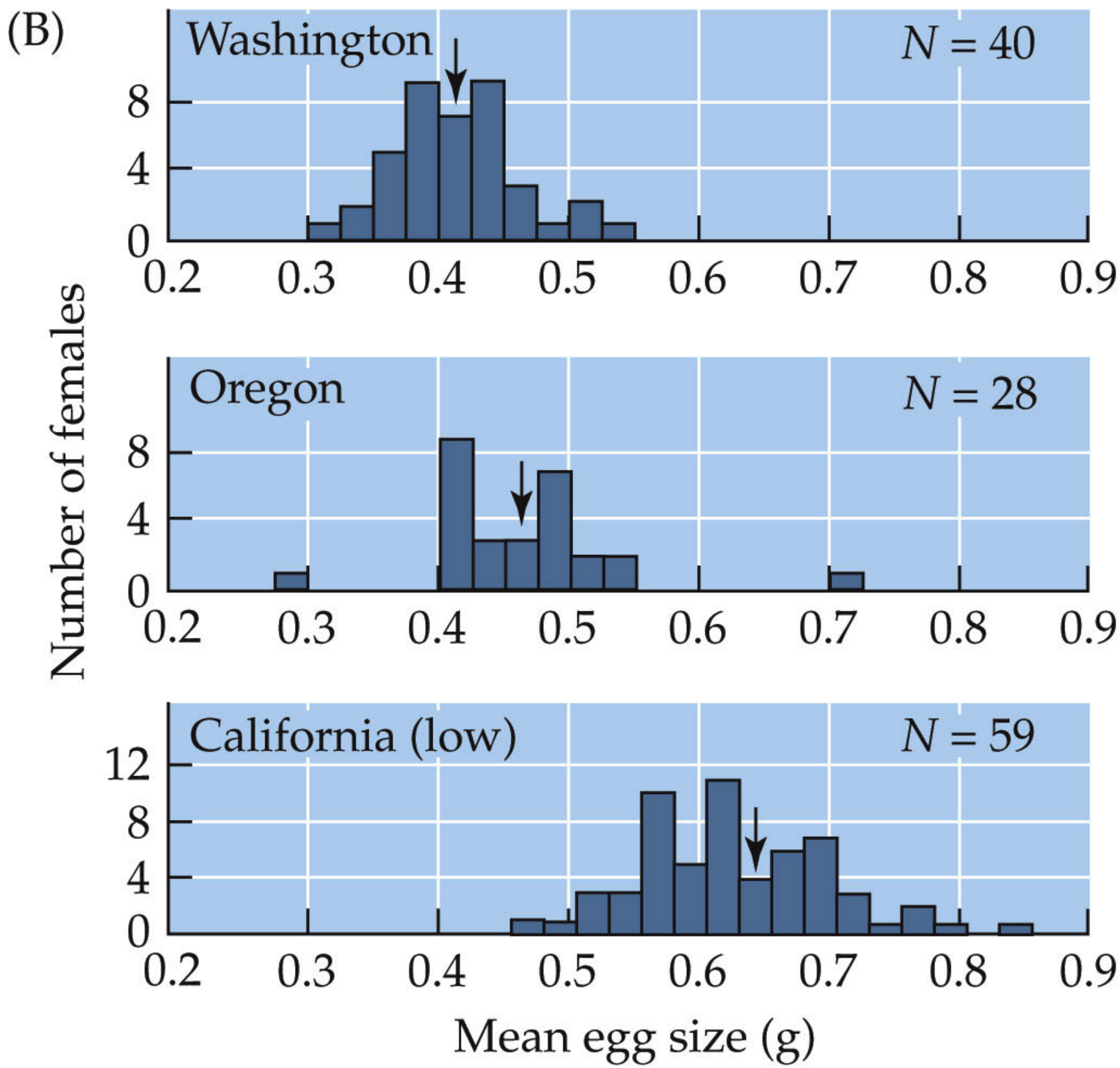
Northern populations of western fence lizards have larger average clutch size, but smaller eggs, than southern populations.

Figure 7.16 Egg Size–Egg Number Trade-Off in Fence Lizards (Part 1)



ECOLOGY, Figure 7.16 (Part 1)

Figure 7.16 Egg Size–Egg Number Trade-Off in Fence Lizards (Part 2)



ECOLOGY, Figure 7.16 (Part 2)

Trade-Offs

Experiments by Sinervo (1990) on the lizard eggs showed that smaller eggs developed faster and produced smaller hatchlings.

The small hatchlings grew faster, but were not able to sprint as fast to escape predators.

Trade-Offs

Selection may favor early hatching in the north, because of shorter growing seasons.

Or faster sprinting speed in the south where there may be more predators.

Trade-Offs

Trade-offs between current and future reproduction:

For an iteroparous organism, the earlier it reproduces, the more times it can reproduce over its lifetime.

But not all reproductive events are equally successful. Often the number of offspring produced increases with size and age of the organism.

Trade-Offs

Atlantic cod increase reproductive output with age.

At 80 cm length, a female produces about 2 million eggs per year. At 120 cm, 15 million eggs per year.

Trade-Offs

Overfishing in the Atlantic has resulted in evolutionary change in the cod's life history.

Fishing selectively removes the older, larger fish, which has led to significant reductions in growth rates and in age and size at maturity.

Trade-Offs

Because the largest fish have the greatest reproductive potential, fishing has resulted in a reduction in the total quality and quantity of egg production.

This change may persist even if overfishing ends, and may delay or prevent recovery of cod populations.

Trade-Offs

If sexual maturity can be delayed, an organism can invest more energy in growth and survival, and may increase its lifetime reproductive output.

Example: A fish with a 5-year lifespan can increase its total reproductive output by delaying maturation by one year, *if* it has a good chance of surviving to age 5.

Trade-Offs

	# Offspring	# Offspring
Year 1	10	
Year 2	20	30
Year 3	30	40
Year 4	40	50
Year 5	50	60
	Total = 150	Total = 180

Trade-Offs

Under what conditions should an organism allocate energy to growth rather than reproduction?

Long life span, high adult survival rates, and increasing fecundity with body size.

If rates of adult survival are low, future reproduction may never occur, so early reproduction rather than growth would be favored.

Trade-Offs

Senescence—decline in fitness of an organism with age and physiological deterioration.

Onset of senescence can set an upper age limit for reproduction.

Semelparous species undergo very rapid senescence and death following reproduction.

Trade-Offs

In some large social mammal species, such as African elephants, postreproductive individuals contribute significantly through parental and grandparental care or contribute to the success of the social group in other ways.

Trade-Offs

Senescence may occur earlier in populations with high mortality rates due to disease or predation.

The mutation accumulation hypothesis of Medawar (1952) suggests that when few individuals survive long enough for selection to act against deleterious mutations that are expressed late in life, these mutations will accumulate.

Trade-Offs

Delayed senescence has been shown in populations of guppies with low mortality rates (Reznick et al. 2004).

In populations where mortality is high due to predation or starvation, guppies may be investing less energy in immune system development and maintenance, resulting in higher rates of senescence due to disease.

Concept 7.4: Organisms face different selection pressures at different life cycle stages.

Different morphologies and behaviors are adaptive at different life cycle stages.

Differences in selection pressures over the course of the life cycle are responsible for some of the distinctive patterns of life histories.

Life Cycle Evolution

Small early life stages are vulnerable to predation.

Small size means less capacity to store nutrients, so they are also vulnerable to competition for food, or environmental conditions that reduce food supplies.

But small size can allow early stages to do things that are impossible for adult stages.

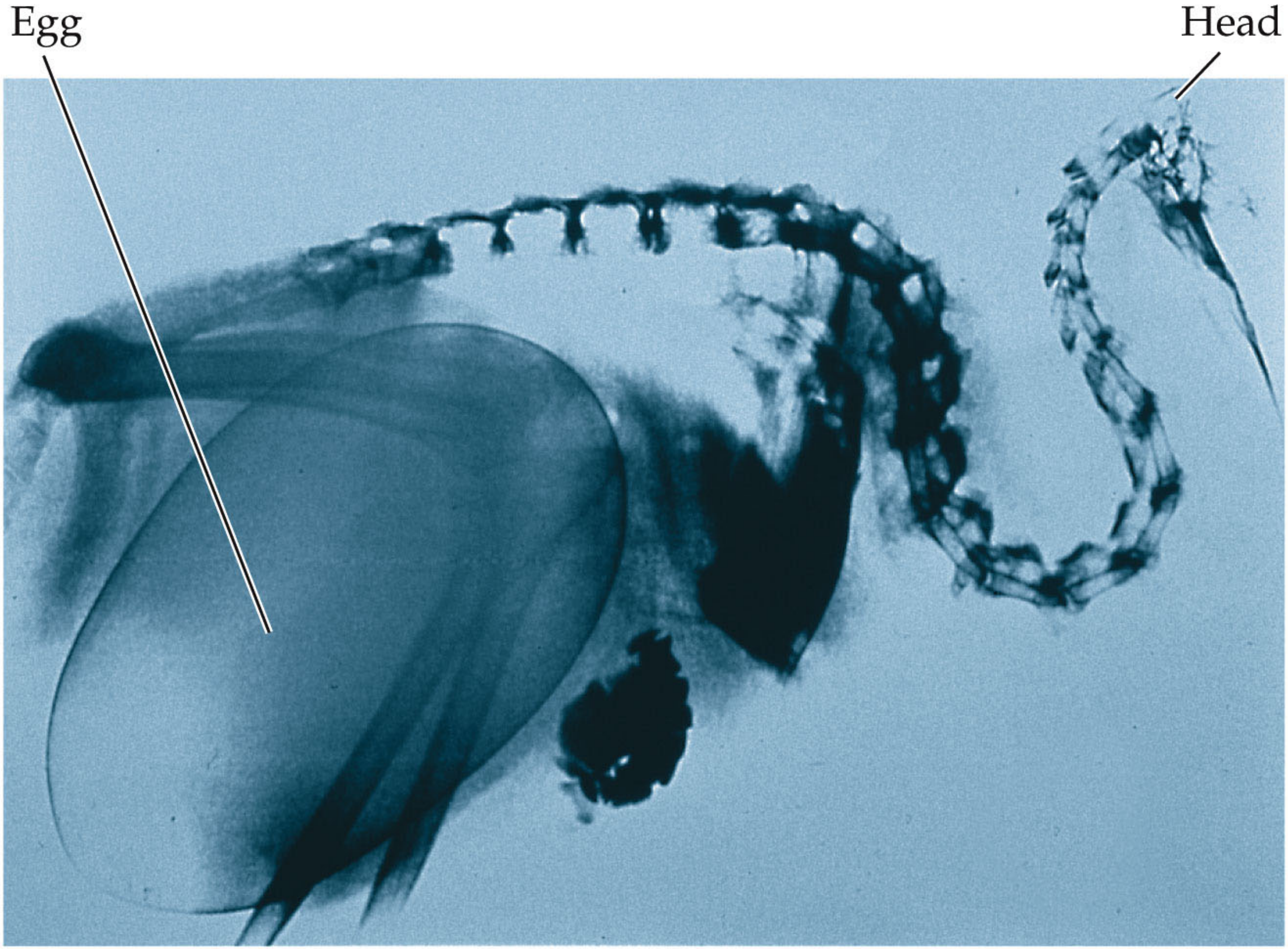
Organisms have various mechanisms to protect the small life stages.

Parental Investment:

Many birds and mammals invest time and energy to feed and protect offspring.

Other species provide more nutrients in eggs or embryos (e.g., in the form of yolks).

Figure 7.18 Parental Investment in the Kiwi



ECOLOGY, Figure 7.18

Plant seeds may have a large **endosperm**, the nutrient-rich material that sustains the embryo during germination (e.g., the milk and meat of coconuts).

Dispersal and diapause:

Small offspring are well-suited for dispersal.

Dispersal can reduce competition among close relatives, and allow colonization of new areas.

Dispersal can allow escape from areas with diseases or high predation.

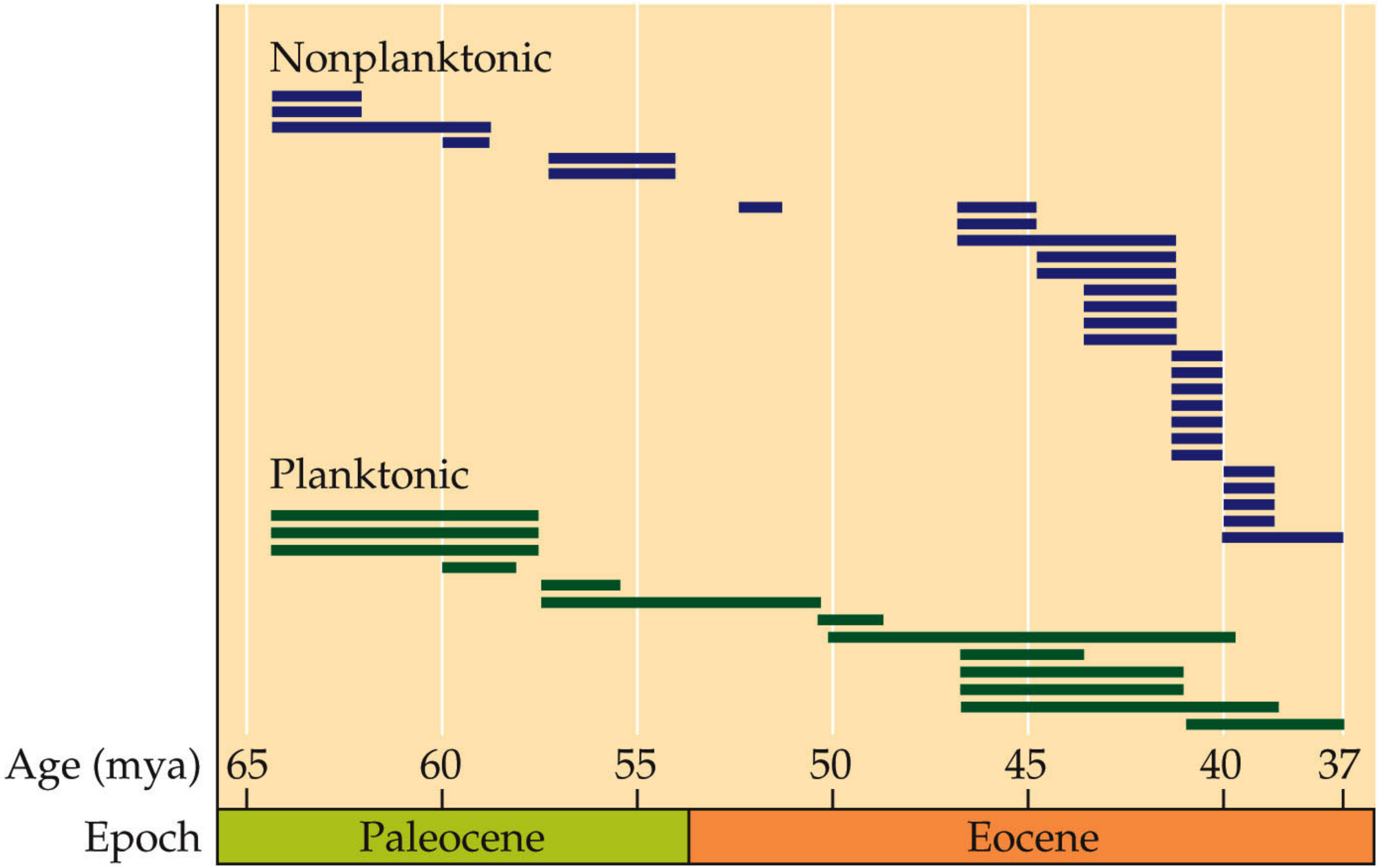
Sessile organisms such as plants, fungi, and marine invertebrates disperse as gametes or larvae—small and easily carried on wind or water currents.

Dispersal has evolutionary significance.

Hansen (1978) compared fossil records of gastropod species with swimming larvae versus species whose larvae developed directly into crawling juveniles.

Direct-developing species tended to have smaller geographic distributions and were more prone to extinction.

Figure 7.19 Developmental Mode and Species Longevity



Diapause: State of suspended animation or dormancy—organisms can survive unfavorable conditions.

Many seeds can survive long dormancy periods.

Many animals can also enter diapause.

Life Cycle Evolution

Amoeboid protists form a hard shell or cyst that allows them to survive dessication.

"Sea monkeys" are brine shrimp eggs that can survive out of water for years.

Small size is advantageous for diapause because less metabolic energy is needed to stay alive.

Life Cycle Evolution

Different life history stages can evolve independently in response to size- and habitat-specific selection pressures.

Complex life cycles minimize the drawbacks of small, vulnerable early stages.

Functional specialization of stages is a common feature of complex life cycles.

Many insects have a larval stage that remains in a small area, such as on a single plant.

The larvae are specialized for feeding and growth, and have few morphological features other than jaws.

Life Cycle Evolution

The adult insect is specialized for dispersal and reproduction.

Some adults, such as mayflies, are incapable of feeding and live only a few hours.

Life Cycle Evolution

In marine invertebrates, larvae are specialized for both feeding and dispersal in ocean currents.

Many larvae have specialized feeding structures called ciliated bands covering most of the body.

They may also have spines, bristles, or other structures to deter predators.

Figure 7.20 Specialized Structures in Marine Invertebrate Larvae

Even in organisms without abrupt shifts between life stages, different sized and aged individuals may have very different ecological roles.

A size- or stage-specific ecological role has been called an **ontogenetic niche** by Werner and Gilliam (1984).

Life Cycle Evolution

In species with metamorphosis, there should be a theoretical optimal time for life stage transitions.

Werner suggested this should occur when the organism reaches a size at which conditions are more favorable for its survival or growth in the adult habitat than in the larval habitat.

Life Cycle Evolution

The Nassau grouper is an endangered coral reef fish. The juvenile stages stay near large clumps of algae.

Smaller juveniles hide within the algae clumps, larger ones stay in rocky habitats near the clumps.

In experiments with these fish, Dahlgren and Eggleston (2000) found that smaller juveniles are very vulnerable to predators in the rocky habitats.

But larger juveniles were not, and were able to grow faster there.

The study support the ideas of Werner—the niche shift was timed to maximize growth and survival.

In some cases metamorphosis is delayed, or eliminated.

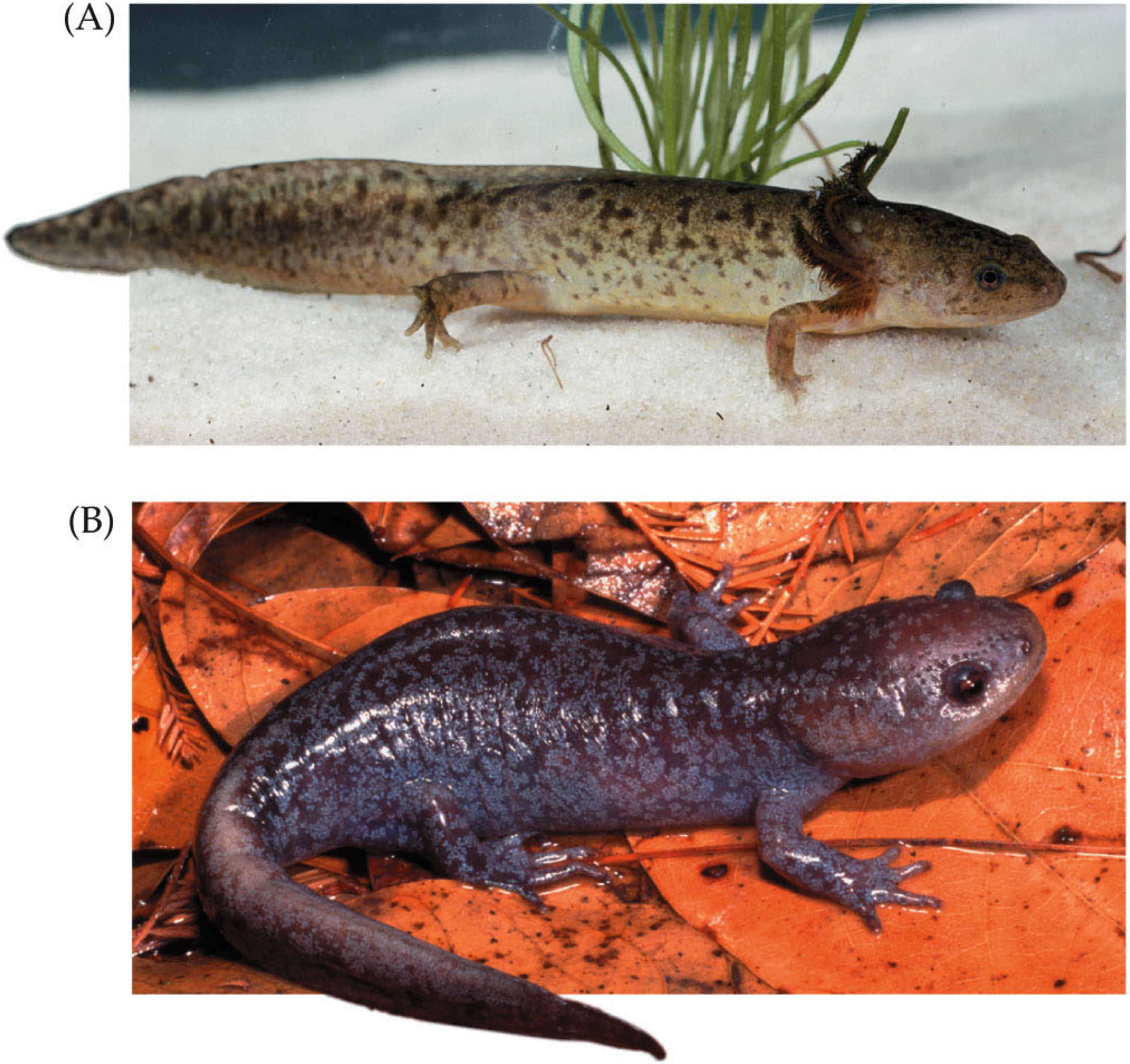
Some salamanders can become sexually mature while retaining larval morphologies and habitat—called **paedomorphic.**

In the mole salamander, both aquatic paedomorphic adults and terrestrial metamorphic adults can exist in the same population.

Figure 7.21 Paedomorphosis in Salamanders

(A)

(B)



Case Study Revisited: Nemo Grows Up

Change in sex during the course of the life cycle is called **sequential hemaphroditism**.

These sex changes should be timed to take advantage of the high reproductive potential of different sexes at different sizes.

Figure 7.22 Sequential Hermaphroditism

Case Study Revisited: Nemo Grows Up

This hypothesis helps to explain sex changes in clownfish and the timing of those changes relative to size.

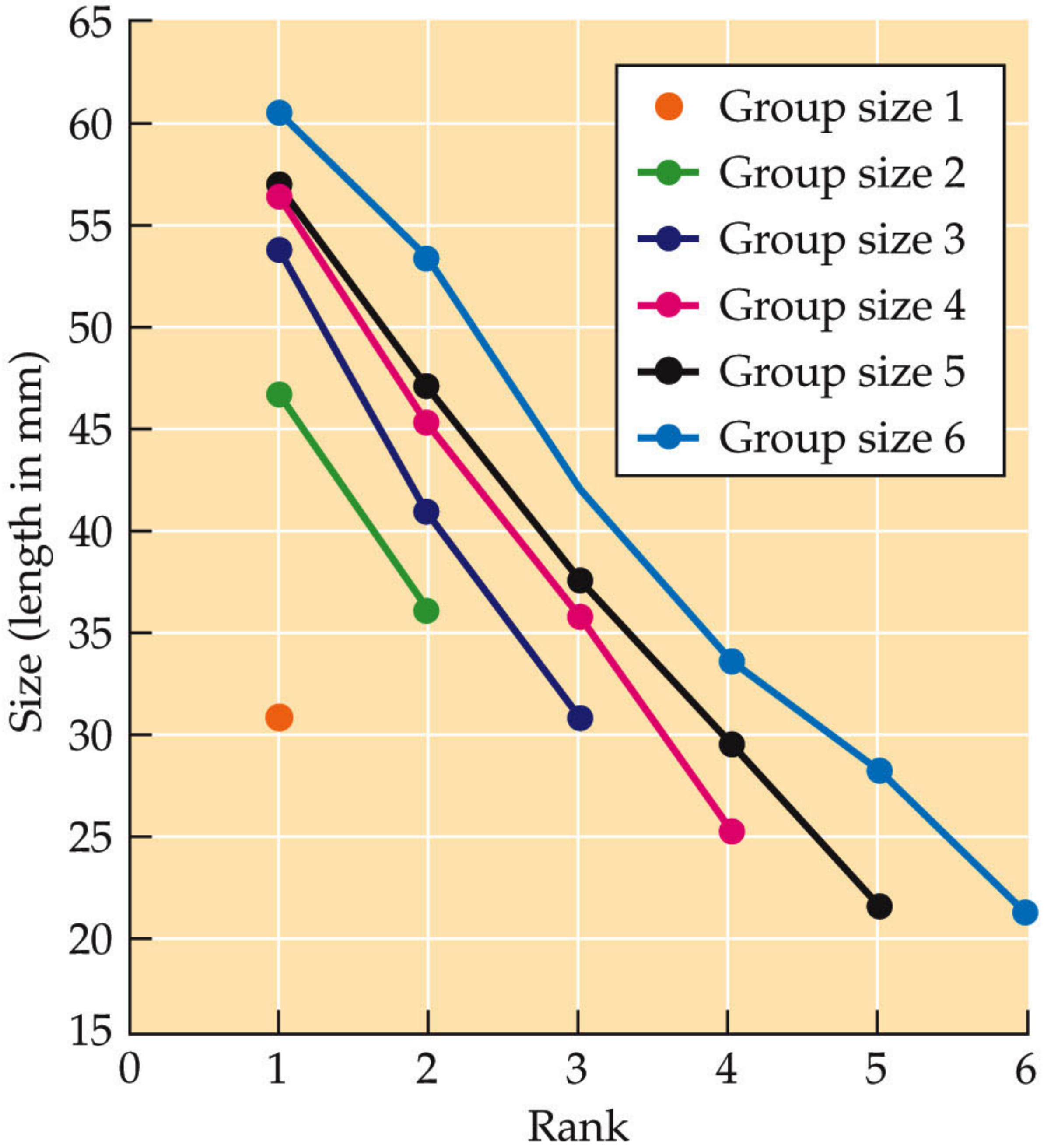
But it does not answer the question of how and why growth is regulated to maintain a hierarchy of clownfish within each anemone.

Case Study Revisited: Nemo Grows Up

Experiments with clownfish show that hierarchy is maintained by regulating growth rates (Buston 2003).

If two fish become similar in size, a fight results and one is expelled from the anemone.

Figure 7.23 Clownfish Size Hierarchies



ECOLOGY, Figure 7.23

Case Study Revisited: Nemo Grows Up

Removal of the breeding male from an anemone resulted in growth of the next largest male—but only until it could take the place of the breeding male, not large enough to threaten the female.

The clownfish avoid conflict within their social groups by exerting remarkable control over their growth rates and reproductive status.

Why do the clownfish maintain the hierarchy?

They are completely dependent on protection by the sea anemone. They are easy prey outside the anemone.

Conflicts result in expulsion and death, probably without having reproduced.

So there is strong selection pressure to avoid conflict.

Growth regulation mechanisms have evolved because individuals that avoid growing to a size that necessitates conflict are more likely to survive and reproduce.

Buston found that remaining in an anemone and biding time offered better chance of reproductive success than leaving to find a new anemone.

Sea anemones are a scarce resource for clownfish.

This controls ontogenetic niche shifts. Juveniles returning to the reef must find an anemone that has space, where it will be allowed to stay and enter the hierarchy.

"Settlement lotteries" also affect other species that compete for space.

Long-lived tree species in tropical rain forests compete for space and sunlight.

Success of any one seedling may depend on chance events, such as death of a nearby tree that creates a gap in the canopy.

Connections in Nature: Territoriality, Competition, and Life History

Complex life histories appear to be one way to maximize reproductive success in such highly competitive environments.