Life History Variation
Each species has a different way to complete its life cycle and reproduce.
Variations in life history involve timing and the relative allocation of nutrients among survival, growth, and reproduction throughout the life span.

- Growth, reproduction, and survival represent competing demands for the finite supply of resources available to the organism.
- An increase in energy allocations to one (for example - growth) will result in a decrease in the other two (i.e. reproduction and survival).
- Energy is used first for maintenance (homeostasis), then growth and, finally, reproduction.

Cost/benefit analyses are used to study life history patterns.

Asexual Reproduction

Asexual Reproduction (gameteless)
- **Parthenogenesis:** an unfertilized egg develops into a new individual.
  - Occurs naturally in many invertebrates (e.g., aphids and many hymenopteran insects), and vertebrates (e.g., whip-tailed lizards, and some fishes: it has been recorded in twic in captive sharks). It occurs very rarely in birds, but is unknown in mammals.
- **Asexual Reproduction**
  - Increased genetic diversity: new "more adaptive" alleles are more rapidly spread and may be more rapidly included in your offspring.
  - Decreased impacts from "bad" mutations.
  - Energetically expensive (locating mates, defending mating territories, and rearing young all cost time and effort).
  - Each individual can only contribute half of its genes.

Asexual Reproduction

- **Agamogenesis:** any reproduction that does not involve a male gamete.
  - **Parthenogenesis:** an unfertilized egg develops into a new individual.
  - Occurs naturally in many invertebrates (e.g., aphids and many hymenopteran insects), and vertebrates (e.g., whip-tailed lizards, and some fishes: it has been recorded in captivity in sharks). It occurs very rarely in birds, but is unknown in mammals.
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Asexual Reproduction

Reproduction without meiosis, ploidy reduction, or fertilization: new individuals are genetically the same as a single parent. Animals are multicellular, so there are none that undergo binary fission. Instead, they may undergo:

- **Budding:** growth of offspring from the body of a single parent.
  - Some cnidarians (e.g., hydras) and platyzoans can reproduce by budding. The buds grow into new individuals that then break away from the parent.
- **Fragmentation:** a new organism grows from a fragment of the parent into a mature, fully grown individual.
  - Examples include sponges, turbellarian flatworms, annelid worms ("starfishes"), which need and arm and ≥20% of the central disc to regenerate.
- **Vegetative reproduction:** new independent individuals are formed without germ cells ("eggs" and "sperm").
  - Much more common than budding or fragmentation is the growth of new individuals from a system of "roots" (e.g., sponges, some corals, entoprocts, some tunicates, some hemichordates).

Rotifer Reproduction

- **Bdelloidea:** females are parthenogenetic (produce diploid eggs that hatch into diploid females).
  - **Bdelloidea** also typically parthenogenetic, but:
    - Female produce diploid amictic (without "mixing genes") eggs by mitosis (usually one at a time) that hatch into diploid females.
    - Can reproduce as ovary (ovulated eggs).
    - Food quality/quantity, photoperiod, and temperature influence production of haploid amictic eggs (generally only 1 or 2 generations/year) by meiosis. If unfertilized, these become haploid, non-feeding males.
    - Male: they are found only during brief periods (can mate about 3 h after hatching).
    - Some may start to feed shortly after hatching.
    - Fusion of the male's sperm and the female's ovum results in a germinal pore and reproductive organs.
    - Bivalves are considered to be the only non-parasitic rotifers.
    - Small number (0.5%) are amictic (produce both haploid and diploid eggs).

Life History Patterns

Figure 16.2 The aspects of reproduction studied by physiologists.
Gender and Sexual Reproduction

Dioecious (or gonochoristic) organisms have either male or female sex organs that produce male or female gametes exclusively (e.g., humans)

Monocious organisms have both male and female sex organs and produce both male and female gametes (e.g., earthworms, some freshwater snails)

- Generally self-fertilization is avoided (e.g., earthworms exchange sperm while mating, but cannot self-fertilize), but some freshwater snails always do.

Hermaphroditic organisms produce bisexual reproductive structures (rare in animals) or change their gender over time, i.e., they are serial (or sequential) hermaphrodites

- Tapeworms produce segments (proglottids) that have both testes and ovaries.
- Only sperm are released from the proglottids and these may enter another proglottid (which may be part of the same or another worm).

Serial (Sequential) Hermaphrodites

Maternal investment in female gamete production and early embryo support requires much more energy and nutrients than sperm production

The most common pattern, therefore, is that younger, smaller individuals are male, while larger, older individuals are female. Many examples, including: sponges, nematodes, some fishes.

In some cases (e.g., marine fishes, such as some groupers), the largest female becomes a male if no male is present

Figure 16.7  Sex change: A bluehead wrasse (Thalassoma bifasciatum) after female and, later, after male.

Sexual Reproduction

Haploid gametes (“egg and sperm”) fuse to form a diploid zygote

- Generally, “male” gametes are:
  - Smaller
  - Contain little if any stored energy reserves
  - Are motile or otherwise able to be widely dispersed

- By contrast, “female” gametes are:
  - Larger
  - Often contain significant energy/nutrient reserves to fuel early development of the offspring
  - Are relatively immobile

Most organisms reproduce sexually

Sexual Size Dimorphism

Unless males defend territories, females tend to be larger.

- For example, many insects, spiders, fishes, and turtles.

However, males that defend territories and breeding opportunities are often larger.

- For example, most lizards, some snakes (e.g., cobras) many mammals: bears, cats, dogs, ruminants, elephants, great apes, seals, some whales.

Mate Associations

A male blue crab will accompany a female for days (fending off other males), attracted by sex pheromones.

In one species of the animal Phylum Echiura, the green spoonworm (Houelia viridis), larvae become females if they do not find an adult female. Otherwise, they enter the female’s urogenital system, remain 1000x smaller, and produce sperm as males.

Male Symbion pandora (Phylum Cycliophora) do not feed and are attached the the females.

Males of deep-sea ceratioid anglerfishes are often parasites on the females.

- The much smaller male bites the female and his lips fuse with her skin.
- Their circulatory systems merge and the female provides both oxygen and nourishment for him after that.
Life History Patterns

1) Reproductive events: their number and whether or not generations overlap:
   - **Monocarpic** (Greek = "one" "fruit"), **Semelparous** (Latin = semel, once, and pario, to beget)
     - Single period of reproduction followed by death, often within the same year (e.g., Pacific salmon and octopods reproduce once but take several years to reach reproductive age)
   - **Polycarpic** (Greek = "many" "fruit"), **Iteroparous** (Latin itero, to repeat, and pario, to beget)
     - Organisms reproduce multiple times over the course of their lives, with overlapping generations, e.g., all birds, humans.

Life History Patterns

2) Length of life: lifespan relative to timing of reproduction
   - **Annuals**: complete life cycle within one year
     - Usually semelparous. Annual life history associated with reproduction at early age and high potential population growth. Adult survival is reduced in disturbed and temporary habitats
     - Fitness increases when the probability that the progeny will establish an adult exceeds the probability that adult will survive another reproductive season. Fitness is maximized in habitats where high reproductive rates are important
   - **Ephemerals** are annuals in temporary habitats (e.g., many desert and arctic species and many temperate zone freshwater species). Iteroparous species (e.g., amphibians may also utilize ephemeral habitats for breeding.

Biennials and Perennials

Perennials: live more than two years
   - Semelparous perennials are relatively rare among animals
     - Pacific salmon (*Oncorhynchus*) hatch in freshwater and migrate downstream to the sea, spending several years feeding and growing. They then swim upstream to mate, lay eggs, and die.
     - American and European eels (*Anguilla*) are born in the Sargasso Sea, the larvae travel to rivers on both sides of the Atlantic and migrate inland as elvers. After several years, they reach adulthood and mate. The females return to the Sargasso to spawn and die.
     - Periodic cicadas spend 7, 11, or 17 years underground as nymphs. As adults, they emerge, mate, lay eggs, and die (no mouthparts). The eggs hatch and the nymphs burrow into the soil.
   - Iteroparous perennials, e.g., most long-lived animals
     - Most energy required for survival.
     - Small amount of reproduction over many years, may produce more offspring in the long run.
     - May reproduce heavily in some years, with little or no reproduction other years, e.g., squirrels reproduce more during mast years for oaks when acorns are abundant.

$r$- vs. $K$-selected life history patterns

3) Mode of life: MacArthur and Wilson (1967) classified organisms according to:
   - Relative rate of increase (growth rate constant of the population, $r$) and
   - Closeness of the population to its carrying capacity ($K$)
Assumes species life histories are distributed along a continuum: $r$-selected species $\rightarrow$ $K$-selected species

"$r$-selected" species
   - Rapid reproduction and short life span ("semelparous annuals")
   - Tend to be smaller and not establish territories
   - Production of numerous small larvae or propagules with long-distance dispersal. Little parental investment in each individual offspring
   - Little energy allocated to growth and survival, most energy allocated to reproduction (which is often explosive)
   - Mortality is density independent (caused by external factors (e.g., drought, frost, fire)
   - Fitness maximized in unpredictable or ephemeral habitats

Figure 16.3: These semelparous species are physiologically programmed to reproduce only a single period of time in their lives.
“K-selected” species

- Slow reproduction and long life span ("iteroparous perennials")
- Tend to be larger and may establish territories
- Production of a reduced number of large offspring with short-distance dispersal
- Energy mostly allocated to growth and survival, little to reproduction (reproduction is spread over a long period of time)
- Mortality is density dependent (caused by crowding or high densities of individuals)
- Fitness maximized in predictable habitats

Survivorship Curves

- Human, whales, elephants
- "K-selected" species

Offspring dormancy and dispersal

Offspring may remain near the parent or be dispersed over long distances (up to 1000s of km)
- Long-distance dispersal (dispersal through space)
  - Zygotes, embryos, or larvae grow quickly after setting in an appropriate location (e.g., beardwrens).
- Short-distance dispersal (e.g., dormant eggs allow dispersal through time, e.g., rotifers, insects, and gemmules of sponges)
  - Stored energy reserve allows life to begin later when conditions are right. Adults may have died off.

Mating Systems

Parental investment
- Males and females differ in the relative size and number of gametes
- Males have many, mobile, and lightweight sperm
- Females have fewer, less-mobile, and heavier eggs

Example: a human female produces a few hundred eggs in her lifetime, whereas a male produces enough sperm to inseminate all the women in the world (Is this really true?)

Two extreme strategies:
- Progeny are immediately abandoned.
- Progeny are nurtured through a significant portion of the parental lifetime.

Reproductive behavior

Differences in parental investment leads to differences in reproductive behavior between males and females

- Females tend to sacrifice opportunities to make more eggs in favor of increasing the chance that each egg will become a viable descendant
- For example, most female mammals shelter and nourish their offspring in uterus and feed them milk long after birth.
- The two species of (now extinct) gastric-brooding frogs incubated the "pre-froglet stages" of their offspring in the stomach of the mother.

Males exhibit less parental investment. Male parenting usually evolves only in those species in which females can’t provide enough energy or time to successfully raise the offspring alone or in species in which males that abandon their mates are unlikely to find another.

- Some exceptions occur, where males not only tend the young but develop physiological adaptations to do so, e.g., seahorses, pipefishes.