CHAPTER 4

Biological Design

Introduction: Size and Shape

Size
- Relationships Among Length, Area, and Volume
- Surface Area
- Volume and Mass

Shape
- Allometry
- Transformation Grids

On the Consequences of Being the Right Size

Biomechanics
- Fundamental Principles
  - *Basic Quantities—Length, Time, and Mass*
  - *Units*
  - *Derived Quantities—Velocity, Acceleration, Force, and Relatives*
  - *Reference Systems*
  - *Center of Mass*
  - *Vectors*
- Basic Force Laws
- Free Bodies and Forces
- Torques and Levers
- Land and Fluid
  - *Life on Land: Gravity*
  - *Life in Fluids*
- Machines
- Strength of Materials
  - *Loads*
  - *Biological Design and Biological Failure*
- Tissue Response to Mechanical Stress
  - *Responsiveness of Bone*

Biophysics and Other Physical Processes
- Diffusion and Exchange
  - *Pressures and Partial Pressures*
  - *Countercurrent, Concurrent, and Crosscurrent Exchange*
- Optics
  - *Depth Perception*
  - *Accommodation*

Overview

Introduction: Size and Shape

Bodies, like buildings, obey laws of physics. Gravity will bring down an ill-designed dinosaur just as certainly as it will fell a faulty drawbridge. Animals must be equipped to address biological demands. The long neck of a giraffe gives it access to treetop vegetation; the claws of cats hook prey; a thick coat of fur gives the bison protection from the cold of winter. In order for animals to catch food, flee from enemies, or endure harsh climates, structures have evolved that serve animals against these challenges to survival. But there is more to an animal's environment than predators and prey, climate and cold. An animal's design must address physical demands. Gravity acts on all structures within its reach. Heavy terrestrial vertebrates must exert much effort to move a massive body from one place to another. Bones and cartilage must be strong enough to bear the weight. If these skeletal structures fail, so does the organism, and its survival is at risk. Animals at rest or in motion experience forces that their structural systems must withstand. As the British biologist J. B. S. Haldane put it,

> "It is easy to show that a hare could not be as large as a hippopotamus, or a whale as small as a herring. For every type of animal there is a most convenient size, and a large change in size inevitably carries with it a change in form."
>
> (Haldane, 1956, p. 952)

In this chapter we examine how structures built by humans and those evolved by natural selection have design features that incorporate and address common problems posed by basic physical forces. For example, living organisms come in a great variety of sizes (figure 4.1); however, not all designs work equally well for all sizes (figure 4.2).

A grasshopper can jump a hundred or more times its own body length. From time to time, this feat has tempted some people to proclaim that if we were grasshoppers we could leap tall buildings in a single bound. The implication is that grasshoppers possess special leaping devices absent in humans. Certainly grasshoppers have suitably long legs that launch them great distances. But the more important reason why grasshoppers and humans differ in their relative jumping abilities is a matter of size, not a matter of long legs. If a grasshopper were enlarged to the size of a human, it too would be unable to leap a hundred times its new body length, despite its long legs. Differences in size necessarily bring differences in performance and in design.

To illustrate this point, let us look at two examples, one from music and one from architecture. A small violin, although shaped generally like a bass, encloses a smaller resonance chamber; therefore, its frequency range is higher (figure 4.3). The larger bass encloses a larger resonance chamber and consequently has a lower frequency range. A Gothic cathedral, because it is large, encloses relatively more space than a small, brick-and-mortar neighborhood church. Large cathedrals include devices to increase surfaces through which light may pass in order to illuminate the congregation within (figure 4.4). The end and sidewalls of cathedrals are designed with outpocketings that architects call apses and transepts. The side walls are pierced by slotted openings, clerestories, and tall windows. Together, apses, transepts, clerestories, and windows allow more light to enter, so they compensate for the proportionately larger volume enclosed within. Later in this chapter, we will see that this principle applies to animal bodies as well.

Shipbuilders often resort to a scale model to test ideas for hull design. But the model, because it is many times smaller than the ship it represents, responds differently to the wave action in a testing tank. Thus, a model alone may not reliably mimic the performance of a larger ship. To compensate, shipbuilders minimize the size discrepancy with a trick—they use slower speeds for smaller models to keep the ship-to-wave interactions about the same as those that large vessels meet on open seas.

Size and shape are functionally linked whether we look inside or outside of biology. The study of size and its consequences is known as **scaling.** Mammals, from shrews to elephants, fundamentally share the same skeletal architecture, organs, biochemical pathways, and body temperature. But an elephant is not just a very large shrew. Scaling requires more than just making parts larger or smaller. As body size changes, the demands on various body parts change disproportionately. Even metabolism scales with size. Oxygen consumption per kilogram of body mass is much higher in smaller bodies. Size and shape are necessarily linked, and the consequences affect everything from metabolism to body design. To understand why, we look first to matters of size.

Size

Because they differ in size, the world of an ant or a water strider and the world of a human or an elephant offer quite different physical challenges (figure 4.5a, b). A human coming out of his or her bath easily breaks the water's surface tension and, dripping wet, probably carries without much inconvenience 250 g (about half a pound) of water clinging to the skin. However, if a person slips in the bath, he or she has to contend with the force of gravity and risks breaking a bone. For an ant, surface tension in even a drop of water could hold the insect prisoner if it were not for properties of its chitinous exoskeleton that make it water repellent. On the other hand, gravity poses little danger. An ant can lift 10 times its own weight, scamper upside down effortlessly across the ceiling, or fall long distances without injury. Generally, the larger an animal, the greater the significance of gravity. The smaller an animal, the more it is ruled by surface forces. The reason for this has little to do with biology. Instead, the consequences of size arise from geometry and the relationships among length, surface, and volume. Let us consider these.

Relationships Among Length, Area, and Volume

If shape remains constant but body size changes, the relationships among length, surface area, volume, and mass change. A cube, for instance, that is doubled in length and then doubled again is accompanied by larger proportional changes in surface and volume (figure 4.6a). Thus, as its length doubles and redoubles, its edge length increases by first 2 and then 4 cm, or factors of 2 and 4. However, the total surface area of its faces increases by factors of 4 and 16. The cube's volume increases in even faster steps, by factors of 8 and 64, for the doubling and redoubling. The shape of the cube stays constant, but because, and *only* because, it is larger, the biggest cube encloses relatively more volume per unit of surface area than does the smallest cube. In other words, the biggest cube has relatively less surface area per unit of volume than the smallest cube (figure 4.6b).

It is certainly no surprise that a large cube has, in *absolute* terms, more total surface area and more total volume than a smaller cube. But notice the emphasis on *relative* changes between volume and surface area, and between surface area and length. These are a direct consequence of changes in size. These relative changes in surface area in relation to volume have profound consequences for the design of bodies or buildings. Because of them, a change in size inevitably requires a change in design to maintain overall performance.

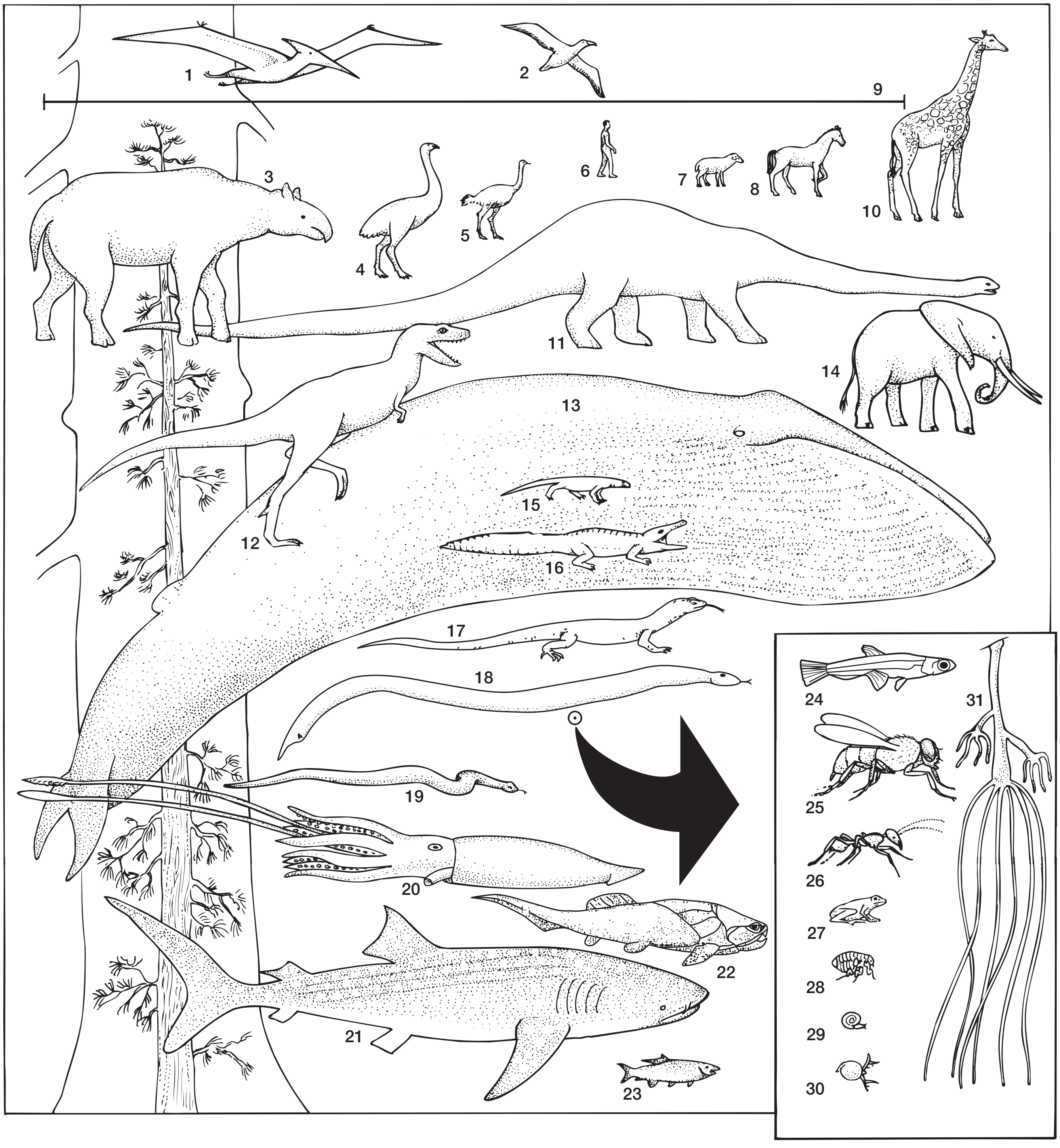


FIGURE 4.1 Animal sizes range over many orders of magnitude. The largest animal is the blue whale, the smallest adult vertebrate a tropical frog. All organisms are drawn to the same scale and are numbered as follows: (1) the pterosaur *Quetzalcoatlus* is the largest extinct aerial reptile; (2) the albatross is today the largest flying bird; a fossil bird (not shown) from South America had an estimated wing span of 20 feet; (3) *Baluchitherium* is the largest extinct land mammal; (4) *Aepyornis* is the largest extinct bird; (5) ostrich; (6) a human figure represented by this scale is 6 feet tall; (7) sheep; (8) horse; (9) this line designates the length of the largest tapeworm found in humans; (10) the giraffe is the tallest living land animal; (11) *Diplodocus* (extinct); (12) *Tyrannosaurus* (extinct); (13) the blue whale is the largest known living animal; (14) African elephant; (15) the Komodo dragon is the largest living lizard; (16) the saltwater crocodile is the largest living reptile; (17) the largest terrestrial lizard (extinct); (18) *Titanoboa* at 43 feet is the longest extinct snake; (19) the reticulated python is the longest living snake; (20) *Architeuthis,* a deep-water squid, is the largest living mollusc; (21) the whale shark is the largest fish; (22) an arthrodire is the largest placoderm (extinct); (23) large tarpon; (24) female *Paedocypris progenetica* from peat swamps of Sumatra; (25) housefly; (26) medium-sized ant; (27) this tropical frog is the smallest tetrapod; (28) cheese mite; (29) smallest land snail; (30) *Daphnia* is a common water flea; (31) a common brown hydra. The lower section of a giant sequoia is shown in the background on the left of the figure with a 100-foot larch superimposed.

After H. G. Wells, J. S. Huxley, and G. P. Wells.

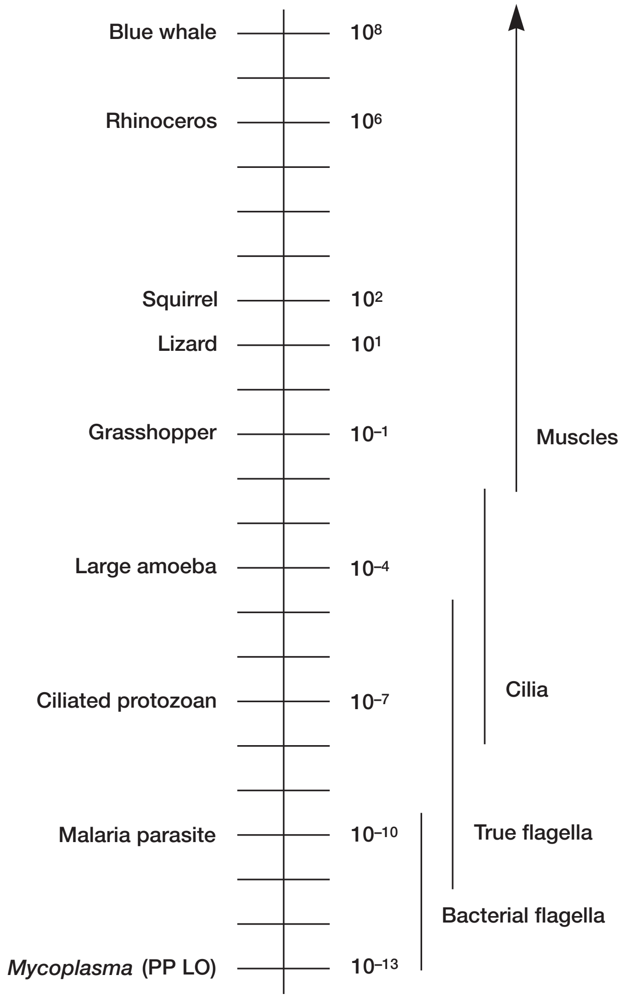


FIGURE 4.2 Body size and locomotion. The masses of living organisms are given on a logarithmic scale. The blue whale tops the scale. *Mycoplasma,* a prokaryotic, bacterium-like organism, is at the bottom. The locomotor mechanism ranges from bacterial flagella to muscle as size increases. Size imposes constraints. Cilia and flagella that move a small mass will become less suitable for locomotion of larger masses. Bigger animals require muscles to drive locomotion.

After McMahon and Bonner.

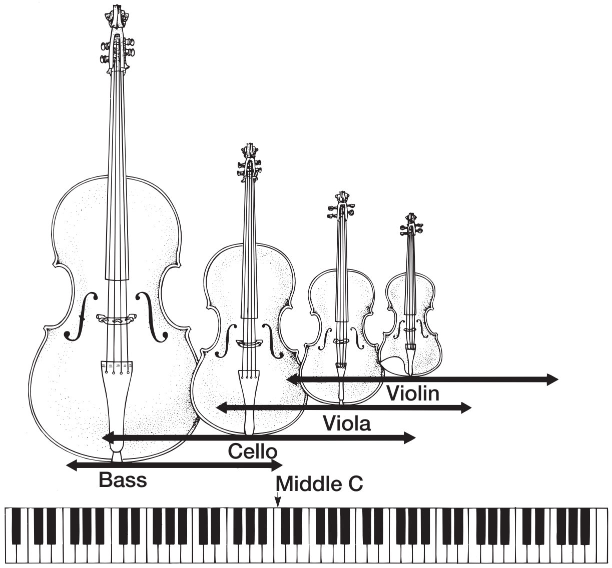
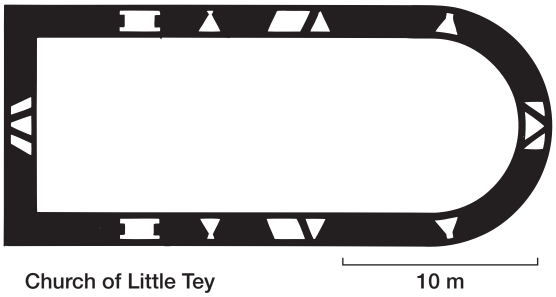


FIGURE 4.3 Influence of size on performance. The four members of the violin family are similarly shaped but they differ in size. Size differences alone produce different resonances and account for differences in performance. The bass is low, the violin high, and the middle-sized cello and viola produce intermediate frequencies.

After McMahon and Bonner.



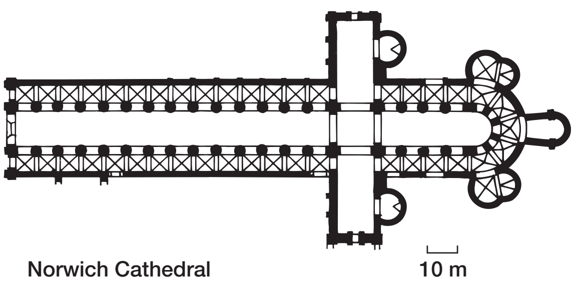


FIGURE 4.4 Influence of size on design. The floor plans of a small medieval church (top) and a large Gothic cathedral (bottom) both in England are drawn to about the same length. The medieval church is about 16 m in length, the Gothic cathedral about 139 m. Because the Gothic cathedral is larger in life, however, it encloses relatively greater space. Transept, chapels, and slotted windows of the sidewalls of the cathedral must let in more light to compensate for the larger volume and to brighten the interior.

For an extended account of the consequences of size on design, see Gould, 1977.

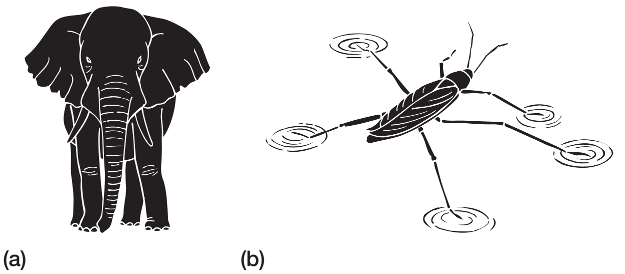


FIGURE 4.5 Consequences of being large or small. Gravity exerts an important force on a large mass. Surface tension is more important for smaller masses. (a) The large elephant has stout, robust legs to support its great weight. (b) The small water strider is less bothered by gravity. In its diminutive world, surface forces become more significant as it stands on water supported by surface tension.

More formally stated, the surface area (S) of an object increases in proportion to ($\propto$) the square of its linear dimensions (l):

$$\boldsymbol{S \propto l^2}$$

But volume (V) increases even faster in proportion to the cube of its linear dimensions (l):

$$\boldsymbol{V \propto l^3}$$

This proportional relationship holds for any geometric shape expanded (or reduced) in size. If we enlarge a sphere, for example, from marble size to soccer ball size, its diameter increases 10 times, its surface increases 10^2 or 100 times, and its volume increases 10^3 or 1,000 times. Any object obeys these relative relationships imposed by its own geometry. A tenfold increase in the length of an organism, as can occur during growth, would bring a 100-fold increase in surface area and a 1,000-fold increase in volume if its shape did not change in the

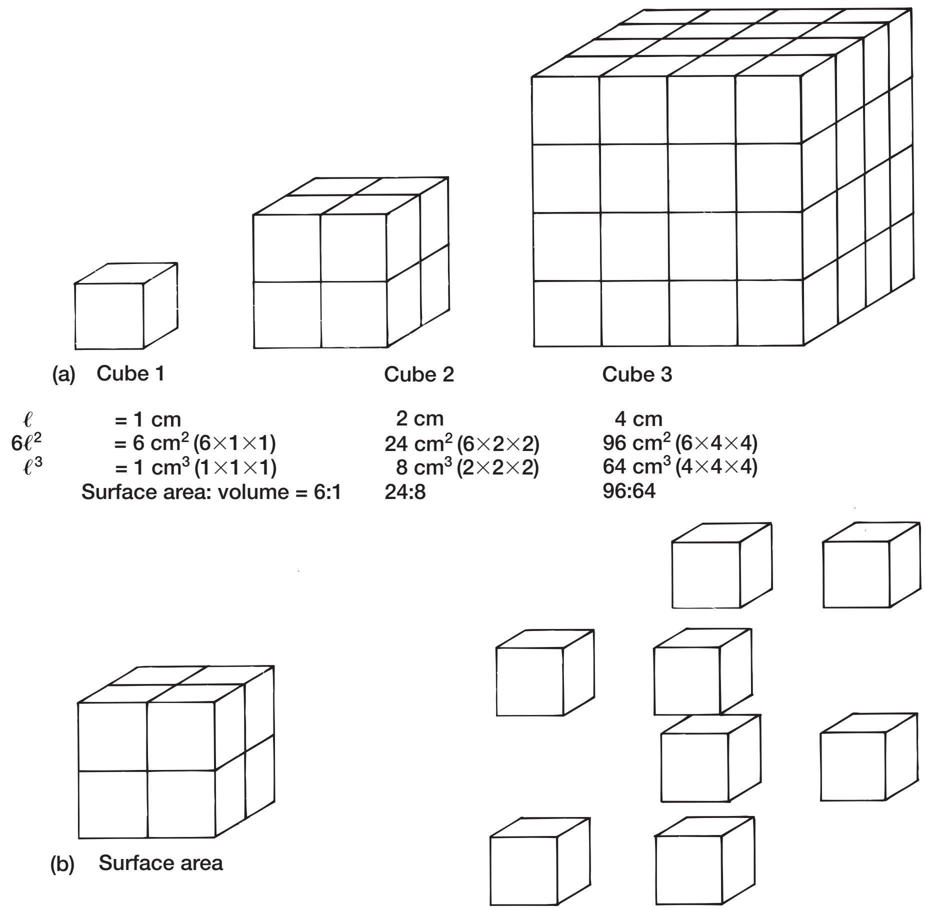


FIGURE 4.6 Length, surface, and volume. (a) Even if shape remains the same, a size increase alone changes the proportions among length, surface, and volume. The length of each edge of the cube quadruples from the smallest to the largest size shown. Cubes 1, 2, and 3 are 1, 2, and 4 cm in length (l) on a side, respectively. The length (l) of a side increases by a factor of 2 as we go from cube 1 to cube 2 and from cube 2 to cube 3. The surface area jumps by a factor of 4 (2^2) with each doubling of length, and the volume increases by a factor of 8 (2^3). A large object has relatively more volume per unit of surface than a smaller object of the same shape. (b) Surface area. By dividing an object into separate parts, the exposed surface area increases. The cube shown on the left has a surface area of 24 cm^2, but when it is broken into its constituents, the surface area increases to 48 cm^2 (8 × 6 cm^2). Similarly, chewing food breaks it into many pieces and so exposes more surface area to the action of digestive enzymes in the digestive tract.

process. So to maintain performance, an organism would have to be designed differently when enlarged simply to accommodate an increase in its volume. Consequently, the same organism is necessarily different when large and must accordingly be designed differently to accommodate different relationships among its length, surface, and volume. With this in mind, let us next turn to surface area and volume as factors in design.

Surface Area

To start a fire, a single log is splintered into many small pieces of kindling. Because the surface area is increased, the fire can start more easily. Similarly, many bodily processes and functions depend on relative surface area. Chewing food breaks it into smaller pieces and increases the surface area available for digestion. The efficient exchange of gases, oxygen and carbon dioxide, for instance, depends in part upon available surface area as well. In gills or lungs, large blood vessels branch into many thousands of tiny vessels, the capillaries, thereby increasing surface area and facilitating gas exchange with the blood. Folds in the lining of the digestive tract increase surface area available for absorption. Bone strength and muscle force are proportional to the cross-sectional areas of parts that particular bones and muscles support or move. Vast numbers of bodily processes and functions depend on relative surface area. These examples show that some designs maximize surface area, while others minimize it. Structures (lungs, gills, intestines, capillaries) that are adapted to promote exchange of materials typically have large surface areas.

Because, as we have seen, surface and volume scale differently with changing size, processes based on relative surface area must change with increasing size. For example, in a tiny aquatic organism, surface cilia stroke in coordinated beats to propel the animal. As the animal gets larger, surface cilia have to move proportionately more volume, so they become a less effective means of locomotion. It is no surprise that large aquatic organisms depend more on muscle power than on ciliary power to meet their locomotor needs. The circulatory, respiratory, and digestive systems rely particularly on surfaces to support the metabolic needs required by the mass of an animal. Large animals must have large digestive areas to ensure adequate surface for assimilation of food in order to sustain the bulk of the organism. Large animals can compensate and maintain adequate rates of absorption if the digestive tract increases in length and develops folds and convolutions. Rate of oxygen uptake by lungs or gills, diffusion of oxygen from blood to tissues, and gain or loss of body heat are all physiological processes that rely on surface area. As J. B. S. Haldane once said: "Comparative anatomy is largely the story of the struggle to increase surface in proportion to volume" (Haldane, 1956, p. 954). We will not be surprised then, when in later chapters we discover that organs and whole bodies are designed to address the relative needs of volume in relation to surface area.

As body size increases, oxygen consumption per unit of body mass decreases (figure 4.7). In absolute terms, a large animal, of course, takes in more total food per day than

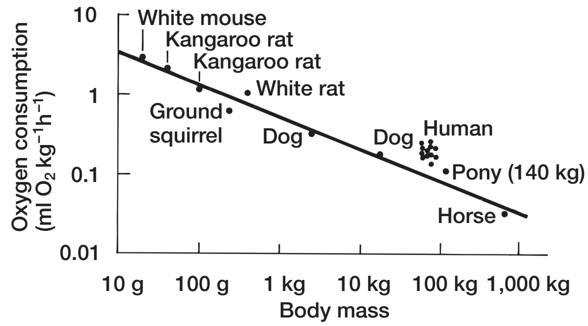


FIGURE 4.7 Relationship between metabolism and body size. Physiological processes, like anatomical parts, scale with size. The graph shows how oxygen consumption decreases per unit of mass as size increases. This is a log-log plot showing body mass along the horizontal scale and oxygen consumption along the vertical. Oxygen consumption is expressed as the volume (ml) of oxygen (O_2) per unit of body mass (kg) during one hour (h).

After Schmidt-Nielsen.

does a small animal to meet its metabolic needs. Certainly, an elephant eats more each day than a mouse does. A cougar may consume several kilograms of food per day, a shrew only several grams. But in relative terms, metabolism per gram is less for the larger animal. The several grams the shrew consumes each day may represent an amount equivalent to several times its body weight; the cougar's daily food intake is a small part of its body mass. Small animals operate at higher metabolic rates; therefore, they must consume more oxygen to meet their energy demands and maintain necessary levels of body temperature. This is partly due to the fact that heat loss is proportional to surface area, whereas heat generation is proportional to volume. A small animal has more surface area in relation to its volume than a larger animal does. If a shrew were forced to slow its weight-specific metabolic rate to that of a human, it would need an insulation of fur at least 25 cm thick to keep warm.

Volume and Mass

When a solid object increases in volume, its mass increases proportionately. Because body mass is directly proportional to volume, mass (like volume) increases in proportion to the cube of a body's linear dimensions.

In terrestrial vertebrates, the mass of the body is borne by the limbs, and the strength of the limbs is proportional to their cross-sectional area. Change in body size, however, sets up a potential mismatch between body mass and cross-sectional limb area. As we learned earlier in this section, mass increases faster than surface area when size increases. A tenfold increase in diameter produces a 1,000-fold increase in mass but only a 100-fold increase in cross-sectional area of the supporting limbs. If shape is unchanged without compensatory adjustments, weight-bearing bones fall behind the

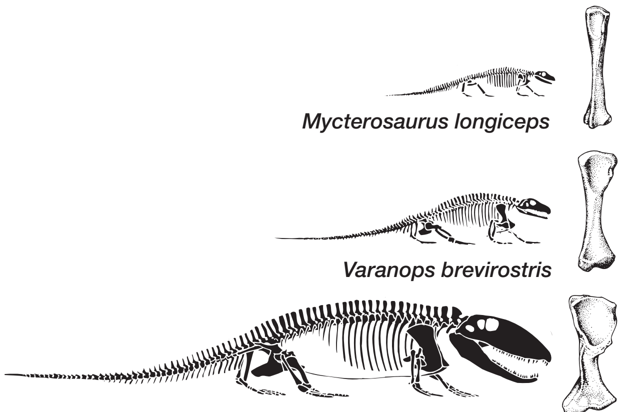


FIGURE 4.8 Body size and limb design in pelycosaurs. Relative sizes of three pelycosaur species are illustrated. The femurs of each, drawn to the same length, are shown to the right of each species. The larger pelycosaur carries a relatively larger mass, and its more robust femur reflects this supportive demand.

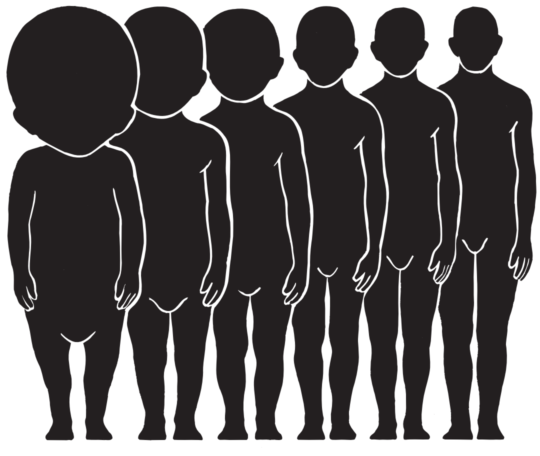


FIGURE 4.9 Allometry in human development. During growth, a person changes shape as well as size. As an infant grows, its head makes up less of its overall height and its trunk and limbs make up more. Ages, in years, are indicated beneath each figure.

From McMahon and Bonner; modified from Medawar.

mass they must carry. For this reason, bones of large animals are relatively more massive and robust than the bones of small animals (figure 4.8). This disproportionate increase in mass compared with surface area is the reason why gravity is more significant for large animals than for small ones.

Whether we look at violins, Gothic cathedrals, or animals, the consequences of geometry reign when it comes to size. Objects of similar shape but different size must differ in performance.

Shape

To remain functionally balanced, an animal must have a design that can be altered as its length and area and mass grow at different rates. As a result, an organism must have different shapes at different ages (sizes).

Allometry

As a young animal grows, its proportions may also change. Young children, too, change in proportion as they grow; children are not simply miniature adults. Relative to adult proportions, the young child has a large head and short arms and legs. This change in shape in correlation with a change in size is called **allometry** (figure 4.9).

Detection of allometric scaling rests on comparisons, usually of different parts as an animal grows. For instance, during growth, the bill of the godwit, a shorebird, increases in length faster than its head. The bill becomes relatively long compared to the skull (figure 4.10). Generally, the relative sizes of two parts, x and y, can be expressed mathematically in the allometric equation

$$y = bx^a$$

where b and a are constants. When the equation is graphed on log-log paper, a straight line results (figure 4.11a, b).

Allometric relationships describe changes in shape that accompany changes in size. Size changes do not occur only during ontogeny. Occasionally, a phylogenetic trend within a group of organisms includes a relative change in size and proportion through time. Allometric plots describe these trends as well. Titanotheres are an extinct group of mammals that comprise 18 known genera from the Early Cenozoic. A plot of skull length versus horn height for each species shows an allometric relationship (figure 4.12). In this example, we track evolutionary changes in the relationship between parts through several species.

Compared with a reference part, the growing feature may exhibit positive or negative allometry, depending on whether it grows faster than (positive) or slower than (negative) the reference part. For example, compared with skull length, the bill of the godwit shows positive allometry. The term **isometry** describes growth in which the proportions remain constant, and neither positive nor negative allometry occurs. The cubes shown in figure 4.6 exemplify isometry, as do the salamanders illustrated in figure 4.13.

Transformation Grids

D'Arcy Thompson popularized a system of transformation grids that express overall changes in shape. The technique compares a reference structure to a derived structure. For instance, if the skull of a human fetus is taken as a reference structure, a rectilinear transformation grid can be used to define reference points at the intersections of the horizontal and vertical grid lines (figure 4.14). These reference points on the fetal skull are then relocated on the adult skull. Next,

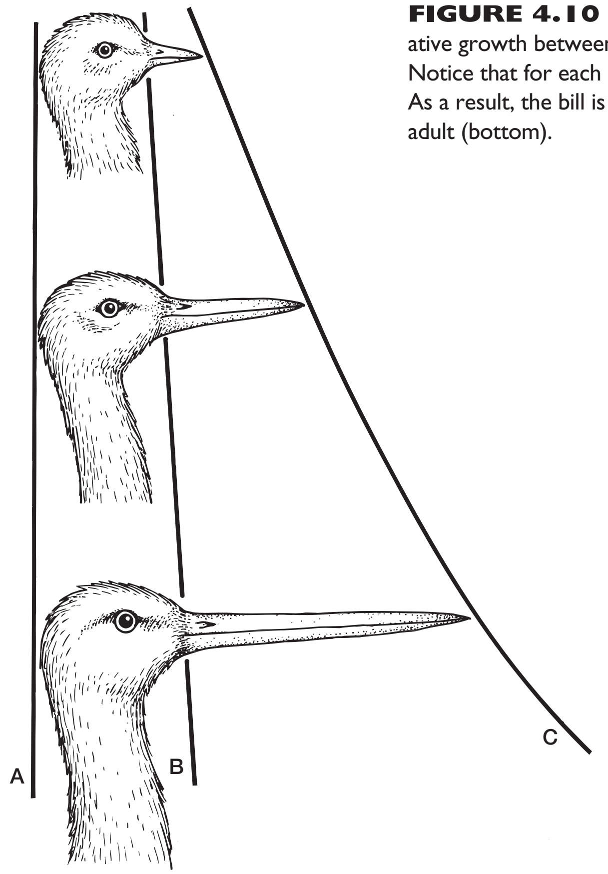
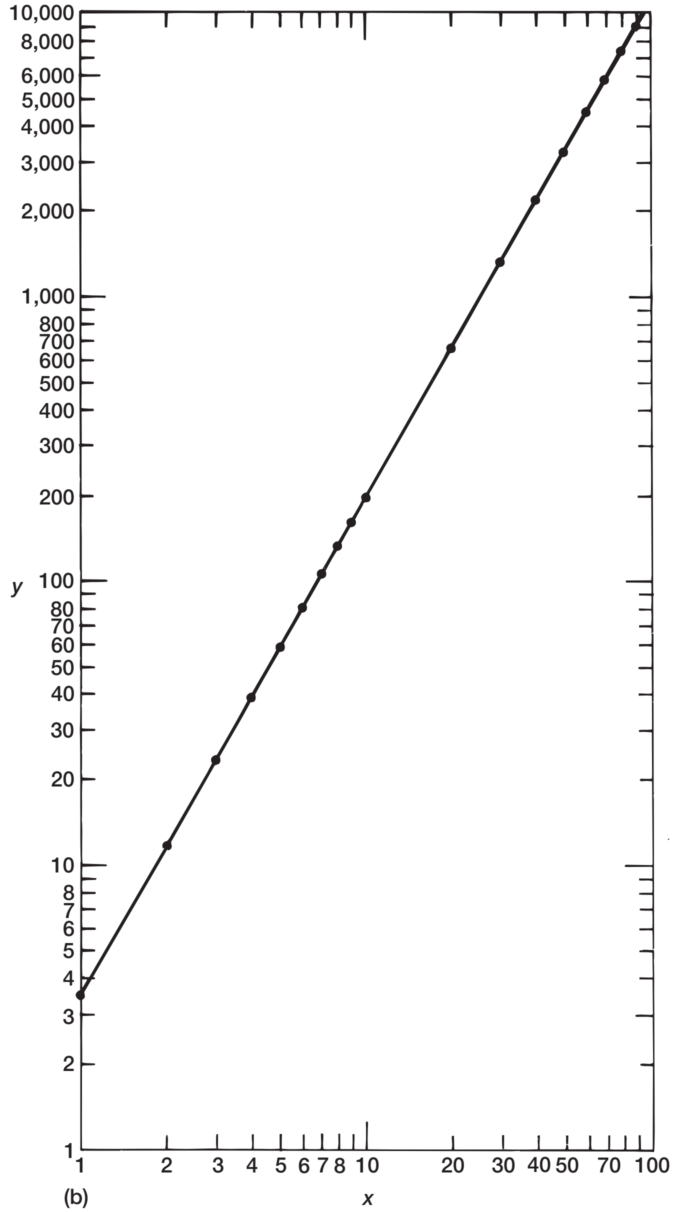


FIGURE 4.10 Allometry in the head of a black-tailed godwit. Differences in relative growth between skull length (lines A and B) and bill length (lines B and C) are compared. Notice that for each increase in skull length, the bill grows in length as well, but at a faster rate. As a result, the bill is shorter than the skull in the chick (top) but longer than the skull in the adult (bottom).

Specimen	Skull dimensions (mm)	
	x	y
A	1	3.5
B	2	11.8
C	3	23.9
D	4	39.6
E	5	58.5
F	6	80.5
G	7	105.4
H	8	133.0
I	9	163.7
J	10	196.8
K	20	662.0
L	30	1,345.9
M	40	2,226.8
N	50	3,290.5
O	60	4,527.2
P	70	5,929.1
Q	80	7,489.9
R	90	9,204.3

(a)



(b)

FIGURE 4.11 Graphing allometric growth. (a) If we organize a range of skulls from the same species in order of size (A–R), we can measure two homologous parts on each skull and collect these data points in a table. (b) If we plot one skull dimension (y) against the other (x) on log-log paper, a line connecting these points describes the allometric relationship between the points during growth in size of the members of this species. This can be expressed with the general allometric equation, $y = bx^a$, wherein y and x are the pair of measurements and b and a are constants, b being the y-intercept and a being the slope of the line. In this example, the slope of the line (a) is 1.75. The y-intercept (b) is 3.5, observed on the graph or calculated by placing the value of x equal to 1 and solving for y. The equation describing the data is $y = 3.5x^{1.75}$.

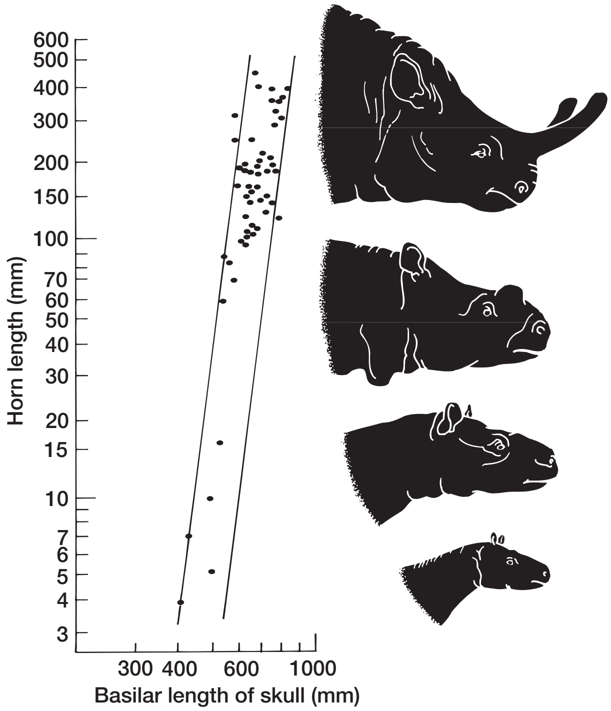


FIGURE 4.12 Allometric trends in phylogeny. The skull and horn lengths of titanotheres, an extinct family of mammals, are plotted. The horn length increases allometrically with increasing size of the skull of each species.

After McMahon and Bonner.

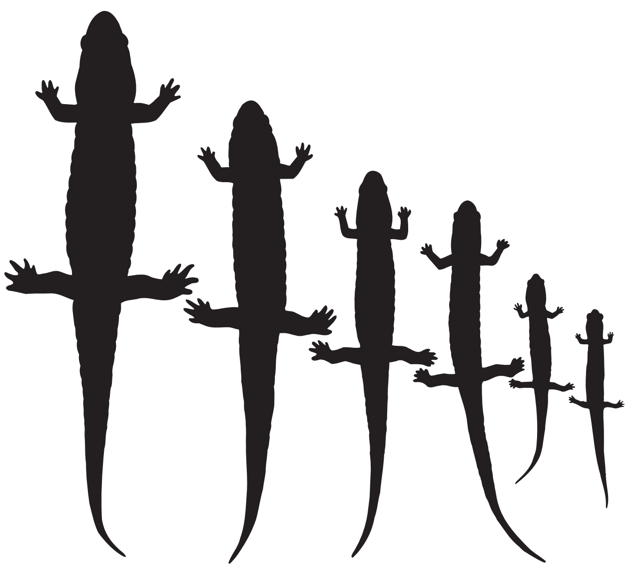


FIGURE 4.13 Isometry. These six species of salamanders differ in size; yet, the smallest is almost the same shape as the largest because body proportions within this genus (*Desmognathus*) remain almost constant from species to species.

Kindly supplied by Samuel S. Sweet, UCSB.

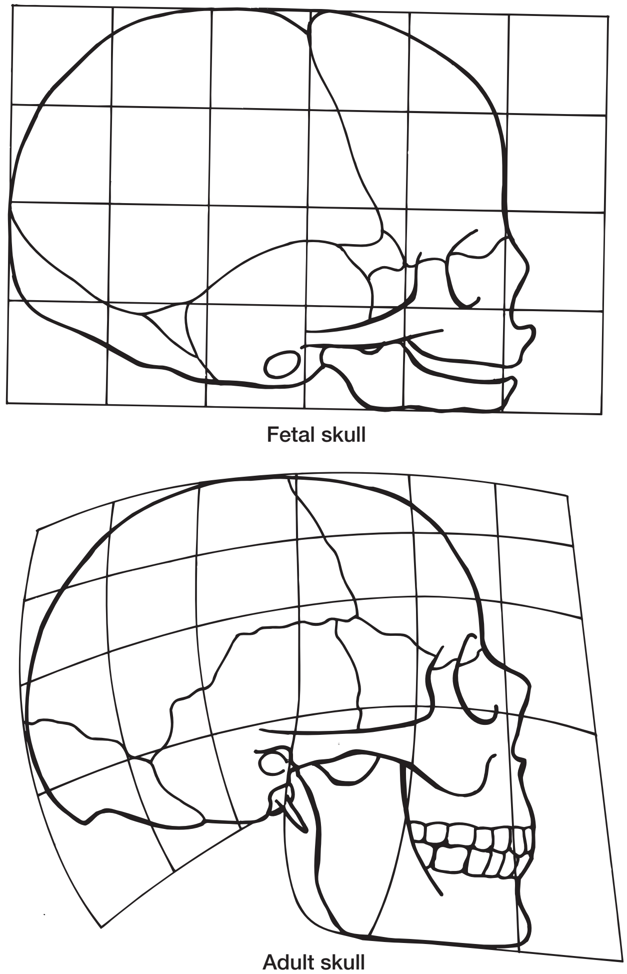


FIGURE 4.14 Transformation grids in ontogeny. Shape changes in the human skull can be visualized more easily with correlated transformation grids. Horizontal and vertical lines spaced at regular intervals can be laid over a fetal skull. The intersections of these lines define points of reference on the fetal skull that can be relocated on the adult skull (bottom) and used to redraw the grid. Because the adult skull has a different shape, the reference points from the fetal skull must be reoriented. A reconstructed grid helps to emphasize this shape change.

After McMahon and Bonner, based on Kummer.

these reference points are connected again to redraw the grid, but because the shape of the skull has changed with growth, the redrawn grid too is differently shaped. Thus, the grid graphically depicts shape changes. Similarly, transformation grids can be used to emphasize, graphically, phylogenetic differences in shape between species, such as the fishes shown in figure 4.15.

Transformation grids and allometric equations do not explain changes in shape; they only describe them. However, in describing changes in proportions, they focus our attention on how tightly shape couples with size.

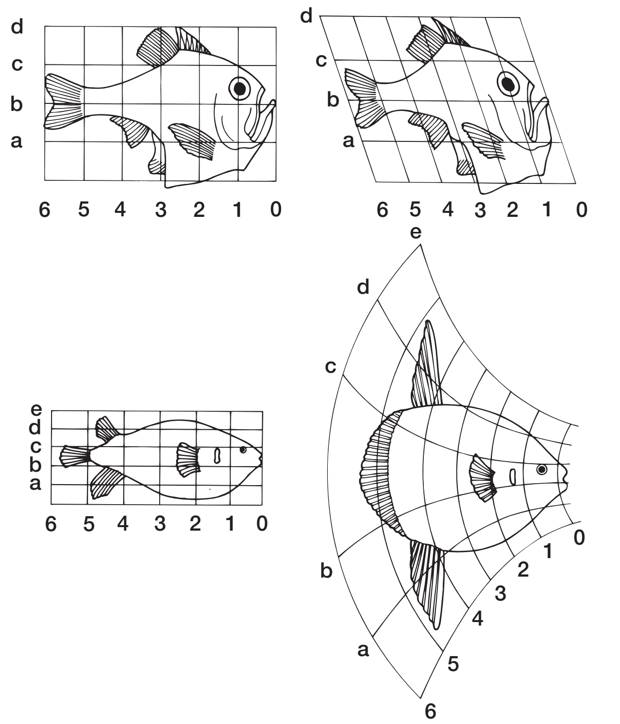


FIGURE 4.15 **Transformation grids in phylogeny.** Changes in shape between two or more species, usually closely related, can also be visualized with transformation grids. One species is taken as the reference (left), and the reference points are relocated in the derived species (right) to reconstruct the transformed grid.

Modified from Thompson.

On the Consequences of Being the Right Size

Animals, large or small, enjoy different advantages because of their sizes. The larger an animal, the fewer are the predators that pose a serious threat. Adult rhinoceroses and elephants are simply too big for most would-be predators to handle. Large size is also advantageous in species in which physical aggression between competing males is part of reproductive behavior. On the other hand, small size has its advantages as well. In fluctuating environments struck by temporary drought, the sparse grass or seeds that remain may sustain a few small rodents. Because they are small, they require only a few handfuls of food to see them through. When the drought slackens and food resources return, the surviving rodents, with their short reproductive and generation times, respond in short order and their population recovers. In contrast, a large animal needs large quantities of food on a regular basis. During a drought, a large animal must migrate or perish. Typically, large animals also have long generation times and prolonged juvenile periods. Thus, populations of large animals may take years to recover after a severe drought or other devastating environmental trauma.

The larger an animal, the more its design must be modified to carry its relatively greater weight, a consequence of the increasing effects of gravity. It is no coincidence that the blue whale, the largest animal on Earth today, evolved in an aquatic environment in which its great weight received support from the buoyancy of the surrounding water. For terrestrial vertebrates, an upper size limit occurs when supportive limbs become so massive that locomotion becomes impractical. The movie creators of Godzilla were certainly unaware of the impracticality of their design as this great beast crashed about stomping buildings. For lots of reasons, not the least of which is his size, Godzilla is an impossibility.

Body parts used for display or defense often show allometry, as the adult ram horns in figure 4.16 illustrate. As a male lobster grows, its defensive claw grows too, but much more rapidly than the rest of its body. When the lobster attains a respectable size, its claw has grown into a formidable weapon (figure 4.17). The claw exhibits **geometric growth;** that is, its length is *multiplied* by a constant in each time interval. The rest of the body shows **arithmetic growth** because a constant is *added* to its length in each time interval. To be effective in defense, the claw must be large, but a young lobster cannot yet wield so heavy a weapon because of its small size. Only after attaining substantial body size can such a claw be effectively deployed in defense. The accelerated growth of the claw brings it in later life up to fighting size. Before that, the small lobster's major defensive tactic is to dash for cover under a rock.

This example shows that size and shape are sometimes linked because of biological function, as with the lobster and its claw. More often, however, design is concerned with the consequences of geometry. Changes in the relationship among length, surface, and volume as an object increases in size (figure 4.6) are the major reason why change in size is necessarily accompanied by change in shape. As we see time and again throughout the book, size itself is a factor in vertebrate design and performance.

Biomechanics

Physical forces are a permanent part of an animal's environment. Much of the design of an animal serves to catch prey, elude predators, process food, and meet up with mates. But biological design must also address the physical demands placed upon the organism. In part, analysis of biological design requires an understanding of the physical forces an animal experiences. Those in the field of **bioengineering** or **biomechanics** borrow concepts from engineering mechanics to address these questions.

Mechanics is the oldest of the physical sciences, with a successful history dating back at least 5,000 years to the ancient pyramid builders of Egypt. It continues up to the present with the engineers who send spaceships to the planets. Through the course of its history, engineers of this discipline have developed principles that describe the physical

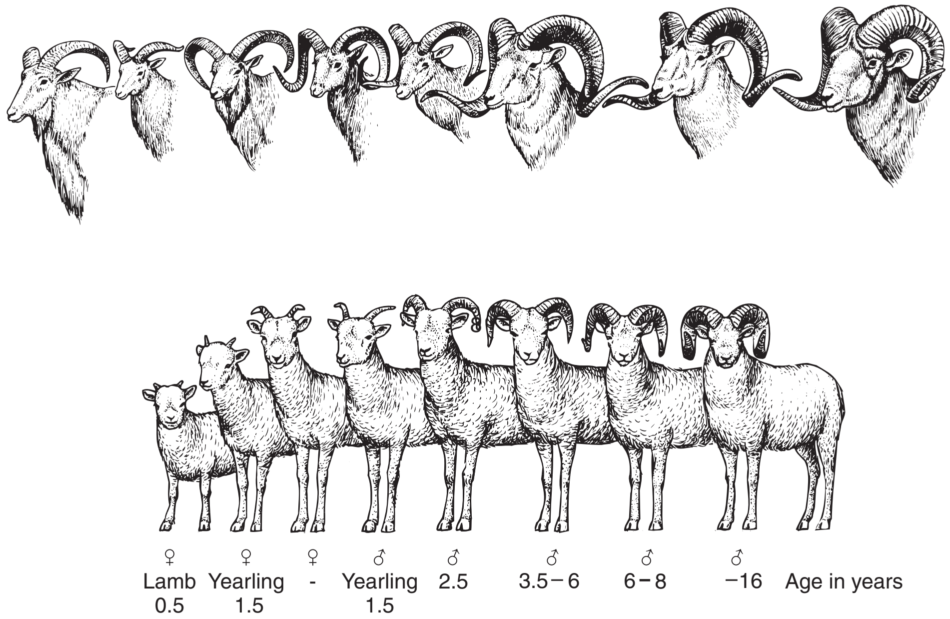


FIGURE 4.16 Changes in horn shape. These species and subspecies of Asiatic sheep show changes in horn shape across their geographic distribution (top). The first in the lineup is the Barbary sheep (*Ammotragus*) from North Africa. The others belong to species or subspecies of *Ovis,* Asiatic sheep of the argali group that extend into central Asia. The last sheep on the right is the Siberian argali (*Ovis ammon ammon*). As a young male bighorn grows in size (bottom illustration), its horns change shape as well. In the adult ram, these horns are used in social displays and in combat with male rivals.

Modified from Geist, 1971.

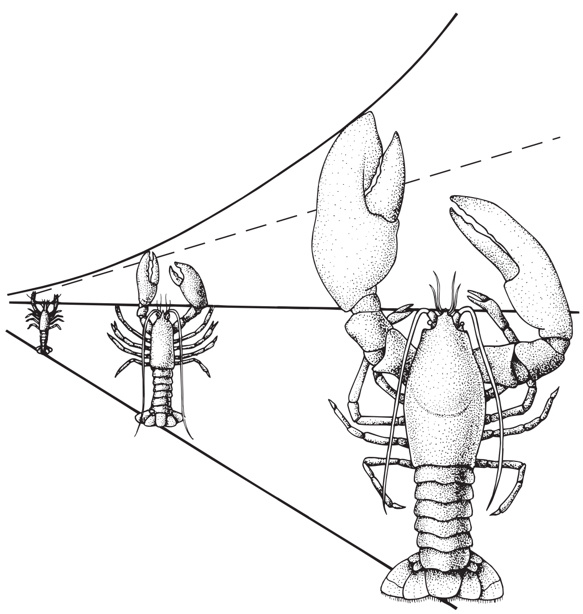


FIGURE 4.17 Lobster allometry. Although the defensive claw is small at first, it grows geometrically while body length increases only arithmetically. Because of this, when the body is large enough to use the claw, the claw has increased dramatically in size to become an effective weapon. The dashed line indicates the size the claw would reach if it did not show allometry; that is, if it grew arithmetically instead of geometrically.

properties of objects, from bodies to buildings. Ironically, engineers and biologists usually work in reverse directions. An engineer starts with a problem, for instance, a river to span, and then designs a product, a bridge, to solve the problem. A biologist, however, starts with the product, for instance, a bird wing, and works back to the physical problem it solves, namely, flight. Nonetheless, reducing animals to engineering analogies simplifies our task of understanding animal designs.

Fundamental Principles

Animals certainly are more than just machines. But the perspective of biomechanics gives a clarity to biological design that we might not otherwise expect. An introduction to a few basic biomechanical principles follows.

Basic Quantities—Length, Time, and Mass

Most of the physical concepts we deal with in biomechanics are familiar. **Length** is a concept of distance, **time** is a concept of the flow of events, and **mass** is a concept of inertia.

Length and time come to us easily. But when it comes to the concept of **mass,** however, our intuition not only fails but actually interferes, because what most people call "weight" is not equivalent to "mass." Mass is a property of matter, weight a measure of force. One way to think of the difference is to consider two objects in outer space, say, a pen and a refrigerator. Both would be weightless and neither would exert a force on a scale. However, both still have mass, although the mass of each is different. To toss the pen to a companion astronaut would require little effort, but to move the massive but weightless refrigerator would require a mighty heave even in the weightlessness of space. Contrary to intuition, therefore, weight and mass are not the same concepts.

Units

Units are not concepts but conventions. They are standards of measurement that, when attached to length, time, and mass, give them concrete values. A photograph of a building alone gives no necessary indication of its size (figure 4.18); therefore, a friend is often pressed into service to stand in the picture to give a sense of scale to the building. Similarly, units serve as a familiar scale. But different systems of units have grown up in engineering, so a choice must be made.

In a few English-speaking countries, mainly the United States, the "English system" of measurement—pounds, feet, seconds—has been preferred. Initially, these units grew up from familiar objects such as body parts. The "inch" was originally associated with the thumb's width, the "palm" was the breadth of the hand, about 3 inches, the foot equaled 4 palms, and so on.

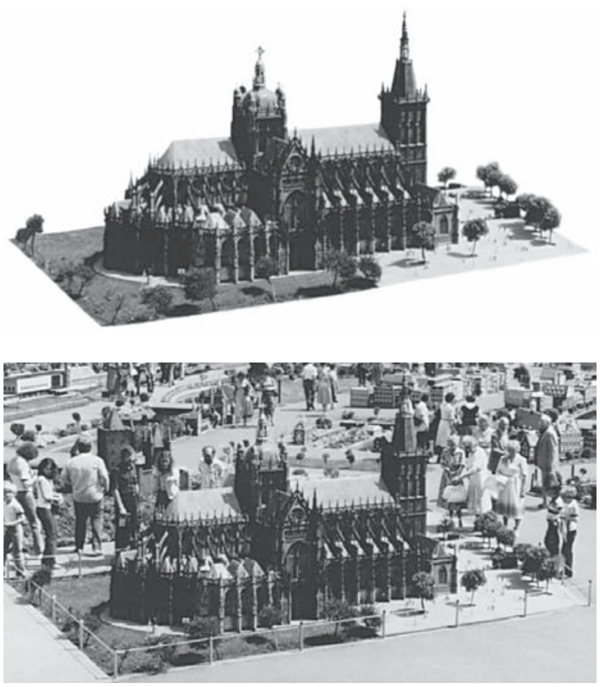


FIGURE 4.18 Units of reference. We use familiar objects as references of size. If denied familiar references, such as fellow humans (top), we can easily overestimate the true size of the cathedral (bottom). Units of measurement such as inches, feet, and pounds are conventions attached to quantities in order for us to set standard references for expressing distances and weight.

Although poetic, the English system can be cumbersome when converting units. For instance, to change miles to yards requires multiplying by 1,760. To convert yards to feet, we must multiply by 3, and to convert feet to inches, we multiply by 12. During the French Revolution, a simpler system based on the meter was introduced. Changing kilometers to meters, meters to centimeters, or centimeters to millimeters requires only moving the decimal point. The **Système Internationale,** or **SI,** is an extended version of the older metric system. Primary units of the SI include meter (m), kilogram (kg), and second (s) for dimensions of length, mass, and time, respectively. In this book, as throughout physics and biology, SI units are used. Table 4.1 lists the common units of measurement in both the English and the SI systems.

Derived Quantities—Velocity, Acceleration, Force, and Relatives

Velocity and **acceleration** describe the motion of bodies. Velocity is the rate of change in an object's position, and acceleration in turn is the rate of change in its velocity. In part, our intuition helps our understanding of these two concepts. When traveling east by car on an interstate highway, we may change our position at the rate of 88 km per hour (velocity) (about 55 mph if you are still thinking in the English system). Step on the gas and we accelerate; hit the brake and we decelerate or, better stated, we experience negative acceleration. With mathematical calculations, negative acceleration is a better term to use than deceleration because we can keep positive and negative signs in a more straightforward way. The sensation of acceleration is familiar to most, but in common conversation, units are seldom mentioned. When they are properly applied, units may sound strange. For instance, suddenly braking a car may produce a negative acceleration of -290 km h^{-2}

TABLE 4.1 Common Fundamental Units of Measurement

English System	Physical Quantity	Système Internationale (SI)
Slug or pound mass	Mass	Kilogram (kg)
Foot (ft)	Length	Meter (m)
Second (s)	Time	Second (s)
Feet/second (fps)	Velocity	Meters/second (m s^{-1})
Feet/second^2 (ft sec^2)	Acceleration	Meters/second^2 (m s^{-2})
Pound (lb)	Force	Newtons (N or kg m s^{-2})
Foot-pound (ft-lb)	Moment (torque)	Newton meters (Nm)

(about -180 mph h^{-1}). The units may be unfamiliar, but the experience of acceleration, like that of velocity, is an everyday event.

Force describes the effects of one body acting on another through their respective mass and acceleration. **Density** is mass divided by volume. Water has a density of 1,000 kilograms per cubic meter (kgm m^{-3}). **Pressure** is force divided by the area over which it acts—pounds ft^{-2} or N m^{-2} for instance. **Work** is the force applied to an object times the distance the object moves in the direction of the force with a joule (after James Joule, 1818–1889) as the unit. Oddly, if the object does not move, much force may be applied but no work is accomplished. A chain holding a chandelier exerts a force keeping the object in place, but if the chandelier remains in position, no displacement occurs so no work occurs. **Power** is the rate at which work gets done, therefore power equals work divided by the time it takes. The unit is the watt (after James Watt, 1736–1819), and one watt is a joule per sec (J s^{-1}).

Common conversation has allowed these terms to drift in meaning, which we need to avoid when we use them in a physical sense. I have already mentioned the misuse of weight (a result of gravity) and of mass (a result of the object's own properties independent of gravity). We might speak of a strong arm squeeze as a lot of force, when our discomfort may in fact result from force per concentrated area—pressure. We might express admiration for a person lifting a weight by saying he or she exerts a lot of power, when in fact we are not talking about the rate of doing work but the force generated to lift the weight. In physical terms, we might speak ambiguously. If we say something is heavy we could mean either it is massive or that it is very dense. Even units have slipped. The calorie listed on food packaging is actually a kilocalorie, but calorie sounds leaner.

Reference Systems

When preparing to record events, a conventional frame of reference is selected that can be overlaid on an animal and its range of activity. But be prepared. A reference system can be defined relative to the task at hand. For instance, when you walk back to the restroom in the tail section of an airplane, you use the plane for reference and ignore the fact that you are really walking forward, with respect to the Earth below. A bird can't get its tail feathers ruffled by flying with a tailwind—it just goes that much faster with respect to the Earth below. For our purposes, and for most engineering applications as well, the coordinate system is usually defined relative to the surface of the Earth.

For reference systems, there are several choices, including the polar and cylindrical systems. The most common, however, is the **rectangular Cartesian reference system** (figure 4.19). For an animal moving in three-dimensional space, its position at any moment can be described exactly on three axes at right angles to each other. The horizontal axis is *x*, the vertical axis is *y*, and the axis at right angles to these is *z*.

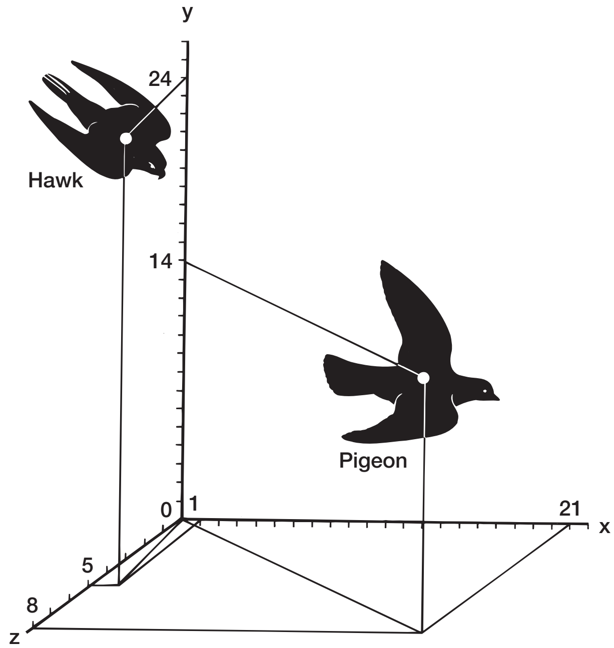


FIGURE 4.19 A three-axis Cartesian coordinate reference system defines the position of any object. Customarily the horizontal, vertical, and axis at right angle to these two are identified as *x, y,* and *z,* respectively. The three intersect at the origin (0). The direct projection line of an object to each axis defines its position at that instant along each axis. Thus, the three projections fix an object's position in space—1, 24, 5 for the hawk and 21, 14, 8 for the pigeon. The white dot graphically represents the center of mass of each bird.

Once defined, the orientation of these reference systems cannot be changed, at least not during the episode during which we are taking a series of measurements.

Center of Mass

If we are interested in the motion of a whole organism rather than the separate motion of its parts, we can think of the mass of the animal as being concentrated at a single point called its **center of mass.** The center of mass, in laypersons' terms the center of gravity, is the point about which an animal is evenly balanced. As a moving animal changes the configuration of its parts, the position of its center of mass changes from one instant to the next (figure 4.20).

Vectors

Vectors describe measurements of variables with a magnitude and a direction. Force and velocity are examples of such variables because they have magnitude (N in the SI, mph in the English system) and direction (e.g., northwesterly direction). A measurement with only magnitude and no direction is a **scalar quantity.** Time duration and temperature have magnitude but no direction, so they are scalar, not vector, quantities. A force applied to an object can also be

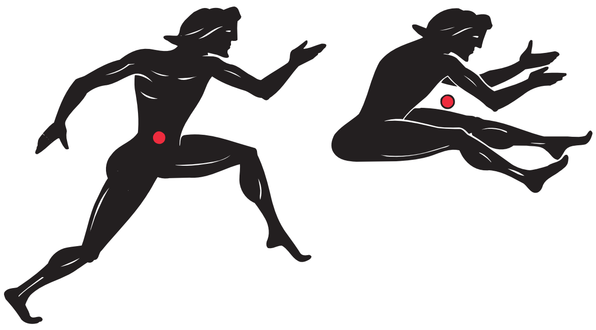


FIGURE 4.20 Center of mass. The single point at which the mass of a body can be thought to be concentrated is the center of mass. As the configuration of this jumper's body parts changes from takeoff (left) to midair (right), the instantaneous location of the center of mass (red dot) changes as well. In fact, note that the center of mass lies momentarily outside the body. A high-jumper or pole-vaulter can pass over the bar even though his or her center of gravity moves under the bar.

represented along a rectangular Cartesian reference system. When we use such a reference system, trigonometry helps us to calculate vector values. For example, we can measure the force applied to a dragged object (F in figure 4.21), but the portion of that force acting horizontally against surface friction (F_x) is more difficult to measure directly. However, given the force (F) and angle (θ), we can calculate both horizontal and vertical components (F_x and F_y). And, of course, conversely, if we know the component forces (F_x and F_y), we can calculate the combined resultant force (F).

Basic Force Laws

Much of engineering is based on laws that were formulated by Isaac Newton (1642–1727). Three of his laws are fundamental:

1. *First law of inertia.* Because of its inertia, every body continues in a state of rest or in a uniform path of motion until a new force acts on it to set it in motion or change its direction. **Inertia** is the tendency of a body to resist a change in its state of motion. If the body is at rest, it will resist being moved, and if it is in motion, it will resist being diverted or stopped.
2. *Second law of motion.* Simply stated, the change in an object's motion is proportional to the force acting on it (figure 4.22). Or, a force (F) is equal to the mass (m) of an object times its experienced acceleration (a):

$$F = ma$$

   Units of this force in newtons (N), kg m s^{-2}, are the force needed to accelerate 1 kg mass at 1 meter per second^2.
3. *Third law of action, reaction.* Between two objects in contact, there is for each action an opposite and equal reaction. Applying a force automatically generates an equal and opposite force—push on the ground and it pushes back on you.

Albert Einstein's (1879–1954) theories of relativity placed limits on these Newtonian laws. But these limitations become mathematically significant only when the speed of an object approaches the speed of light (186,000 miles/s). Newtonian laws serve space travel well enough to get vehicles to the moon and back, and so they will serve us here on Earth as well.

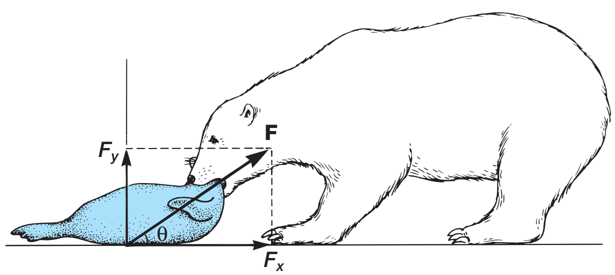


FIGURE 4.21 Vectors. When dragging the seal, the polar bear produces a resultant force (**F**) that can be represented by two small component forces acting vertically (F_y) and horizontally (F_x). The horizontal force acts against surface friction. If we know the resultant force (**F**) and its angle (θ) with the surface, we can calculate the component forces using graphic or trigonometric techniques.

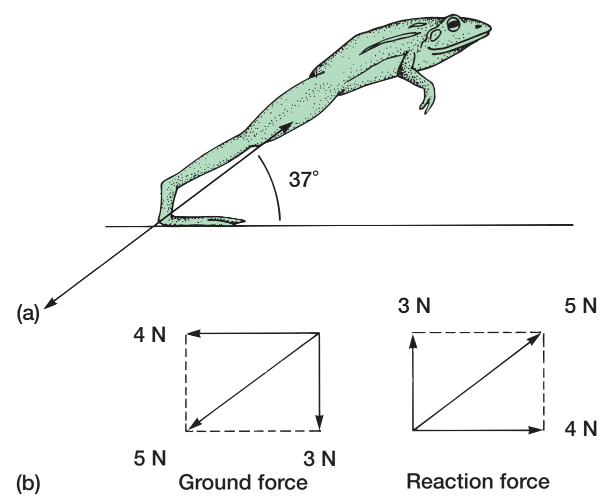


FIGURE 4.22 Forces of motion. (a) The force a frog produces at liftoff is the result of its mass and acceleration at that instant ($F = ma$). (b) Forces produced collectively by both feet of a hefty frog and the ground are opposite but equal. The vector parallelograms represent the components of each force. If a frog of 50 g (.05 kg) accelerates 100 m s^{-2}, a force of 5 N = (100 × .05) is generated along the line of travel. By using trigonometric relations, we can calculate the component forces. If liftoff is at 37°, then these component forces are 4 N = (cos 37° × 5 N) and 3 N = (sin 37° × 5 N).

In biomechanics, Newton's second law, or its modifications, are most often used because the separate quantities can be measured directly. In addition, knowing the forces experienced by an animal often gives us the best understanding of its particular design.

Free Bodies and Forces

To calculate forces, it often helps to isolate each part from the rest in order to look at the forces acting on that part. A **free-body diagram** graphically depicts the isolated part with its forces (figure 4.23a, b).

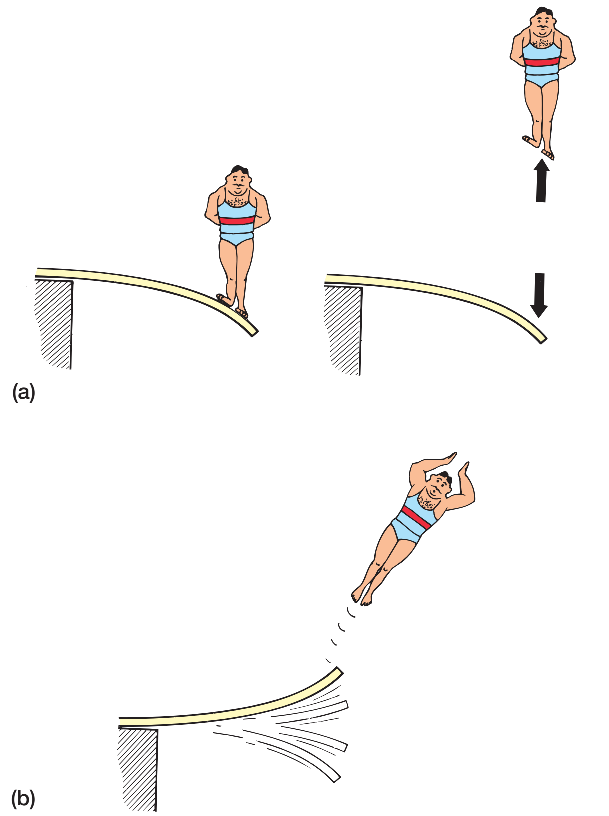


FIGURE 4.23 Free-body diagrams. (a) Two physical bodies, the board and the diver, each exert a force on the other. If the forces of the two bodies are equal, opposite, and in line with each other, then no linear or rotational motion results. Although the forces are present, the two bodies are in equilibrium (left). To depict these forces (right), the two bodies are separated in free-body diagrams, and the forces acting on each body are represented by vectors (arrows). (b) If forces are unequal, motion is imparted. The diver has, by sudden impact, pushed the board down farther than it would go under his weight alone. So it then pushes upward with a force greater than the weight of the diver, and the diver is accelerated upward.

When you walk across a floor, you exert a force upon it. The floor gives ever so slightly and imperceptibly until it returns a force equal to yours, which exemplifies the action and reaction principle described by Newton's third law. If the floor did not push back equally, you would fall through. Think of a diver perched at the end of a diving board. The board bends until it pushes back with a force equal to the force exerted on it by the diver. Diver and board are separated in the free-body diagram, and the forces on each are shown in figure 4.23a. If both forces are equal and opposite, they cancel and the two are in equilibrium. If not, motion is produced (figure 4.23b).

As a practical matter, mechanics is divided between these two conditions. Where all forces acting on an object balance, we are dealing with that part of mechanics known as **statics.** Where acting forces are unbalanced, we are dealing with **dynamics.**

Torques and Levers

In the vertebrates, muscles generate forces and skeletal elements apply these forces. There are several ways to represent this mechanically. Perhaps the most intuitive representation is with torques and levers. The mechanics of torques and levers are familiar because most persons have firsthand experience with a simple lever system, the teeter-totter or seesaw of childhood. Action of the seesaw depends on the opposing weights seated on opposite ends and on the distances of these weights from the pivot point, or **fulcrum.** This distance from weight to fulcrum is the **lever arm.** The lever arm is measured as the perpendicular distance from force to fulcrum. Shorten the lever arm and more weight must be added to keep the board in balance (figure 4.24a). Lengthen it sufficiently, and a little sister can keep several big brothers balanced on the opposite end.

A force acting at a distance (the lever arm) from the fulcrum tends to turn the seesaw about this point of rotation; or more formally, it is said to produce **torque.** When levers are used to perform a task, we also recognize an **in-torque** and **out-torque.** If more output force is required, shortening the "out" and lengthening the "in" lever arms increases the out-torque. Conversely, if out-torque speed (= velocity) or travel distance is required, then lengthening the out and shortening the in lever arms favor greater velocity and distance in the out-torque (figure 4.24c). Of course, this increased speed and distance are achieved at the expense of force in the out-torque. In engineering terms, torque is more commonly described as the **moment** about a point and the lever arm as the **moment arm.**

The mechanics of levers mean that output force and output speed are inversely related. Long output lever arms favor speed, whereas short ones favor force. Regardless of how desirable it would be to have both in the design of, say, an animal's limb, simple mechanics do not permit it. Similarly, long output lever arms sweep through a greater distance, whereas short ones move through a shorter distance. For a given input, both output force and output speed cannot be maximized. Compromises and trade-offs in design must be made.

Consider the forelimbs of two mammals, one a runner specialized for speed, the other a digger specialized to generate large output forces. In figure 4.25a, the relatively long

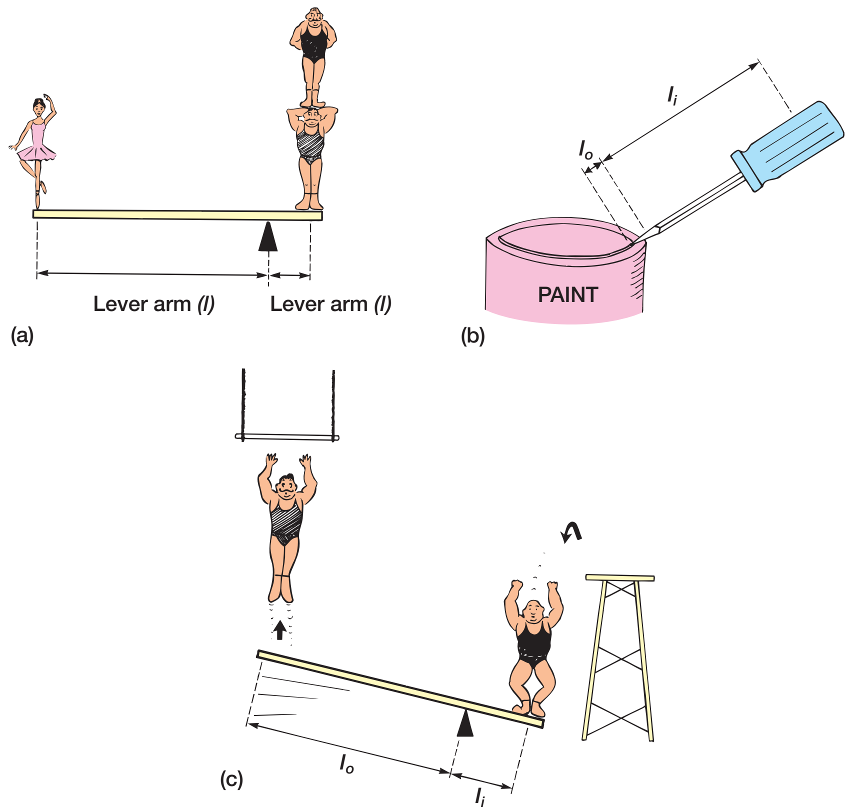


FIGURE 4.24 Principles of lever systems. (a) The balance of forces about a point of pivot (fulcrum) depends on the forces times their distances to the point of pivot, their lever arms (l). (b) To get more output force, the point of pivot is moved closer to the output and farther from the input force. In this diagram, the short output lever arm (l_o) and long input lever arm (l_i) work in favor of more output force. (c) To produce high output speed, the pivot point is moved closer to the input force (l_i). Other things being equal, speed is achieved at the expense of output force.

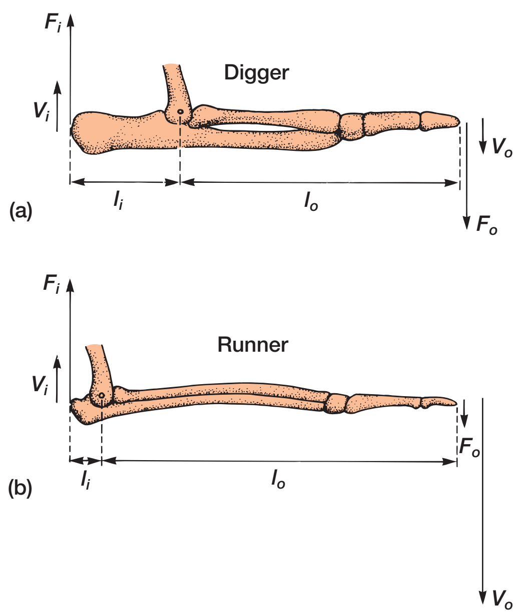


FIGURE 4.25 Strength versus speed. The forearms of a digger (a) and a runner (b) are drawn to the same overall length. Input forces (F_i) and input velocities (V_i) are the same, but output forces (F_o) and velocities (V_o) differ. The differences result from the differences between the lever arm ratios of the two forearms. Output force is greater in the digger than in the runner, but output velocity of the digger is less. Formally, these differences can be expressed as differences in mechanical advantages and in velocity ratios.

elbow process and short forearm of the digger favor large force output. In the runner (figure 4.25b), the elbow is short, the forearm long. Lever arms are less favorable to force output in the forearm of the runner but more favorable to speed. The speed of the elbow is magnified by the relatively greater output lever arm, but this is accomplished at the expense of output force.

More formally, we can express the mechanics of input and output forces at different velocities with simple ratios. The ratio of F_o/F_i, the output to input force, is the **mechanical advantage** (or **force advantage**). The ratio of the output to input lever arms, l_o/l_i, is the **velocity ratio** (or **speed** or **distance advantage**).

As we might expect, diggers enjoy a greater mechanical advantage in their forearm, but runners enjoy a greater velocity advantage in their forearm. There are, of course, other ways of producing output force or speed. Increased size and, hence, force, of input muscles and emphasis of fast-contracting muscle cells both affect output. The lever systems of an animal, in turn, set the relationships between force and speed (or distance).

Artiodactyls, such as deer, have limbs designed to produce both high forces, as during acceleration, and high speed, as when velocity of escape is required (figure 4.26). Two muscles, the medial gluteus and the semimembranosus, with different mechanical advantages, make different contributions to force or to speed output. The medial gluteus enjoys a higher velocity ratio (l_o/l_i = 44, compared

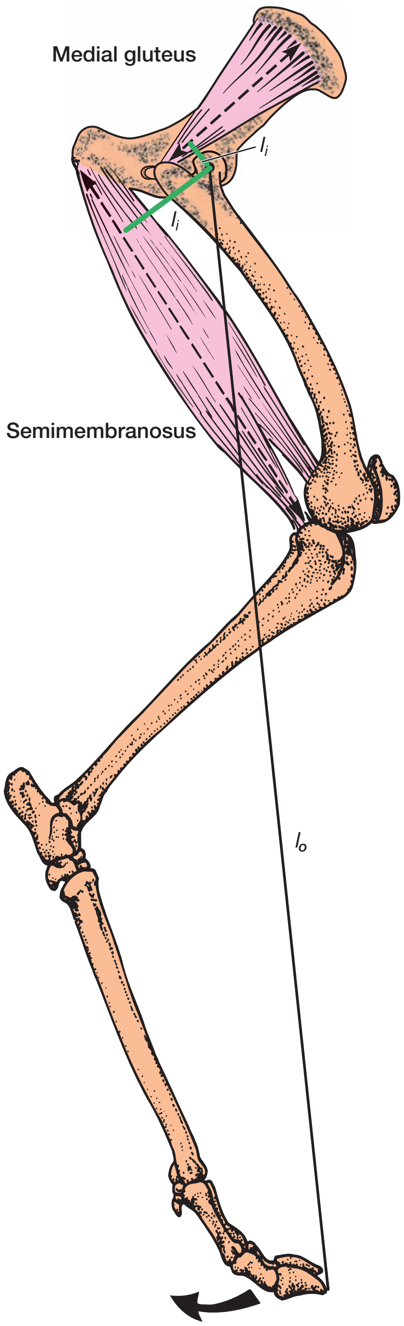


FIGURE 4.26 **High and low gear muscles.** Both the medial gluteus and the semimembranosus muscles turn the limb in the same direction, but they possess different mechanical advantages in doing so. A muscle's lever arm is the perpendicular distance to the point of rotation or pivot point (black dot) from the line of muscle action (dotted line). The velocity ratio is higher in the medial gluteus, which can move the limb faster. But the semimembranosus moves the limb with greater output force because of its longer lever arm. Lever arms in both the muscles (l_i) and the common lever arm out (l_o) are indicated.

After Hildebrand.

with l_o/l_i = 11 for the semimembranosus), a leverage that favors speed. If we compare these muscles with the gears of a car, the medial gluteus would be a "high" gear muscle. On the other hand, the semimembranosus has a mechanical advantage favoring force and would be a "low" gear muscle. During rapid locomotion, both are active, but the low gear muscle is most effective mechanically during acceleration, and the high gear muscle is more effective in sustaining the velocity of the limb.

The two muscles of the deer limb swing it in the same direction. But each muscle acts with a different lever advantage. One is specialized for large forces, the other for speed. This represents one way biological design may incorporate the mechanics of torques and levers to provide the limb of a running animal with some degree of both force and speed output. Just as a seesaw does not have a single fulcrum that can maximize output force and output speed simultaneously, similarly one muscle cannot maximize both. A single muscle has leverage that can maximize either its force output or its speed output, but not both, a limitation that arises from the nature of mechanics, not from any necessity of biology. To work around this, two or more muscles may divide the various mechanical chores amongst them and impart to the limb favorable force, speed, or distance during limb rotation. Biological design must abide by the laws and limits of mechanics when mechanical problems of animal function arise.

Land and Fluid

For terrestrial vertebrates, most external forces they experience arise ultimately from the effects of gravity. Vertebrates in fluids, such as fishes in water or birds in flight, experience additional forces from the water or air around them. Because the forces are different, the designs that address them differ as well.

Life on Land: Gravity

Gravity acts on an object to accelerate it. On the surface of the Earth, the average acceleration of gravity is about 9.81 m s^{-2} acting toward the Earth's center. Newton's second law ($F = ma$) tells us that an animal with a mass of 90 kg produces a total force of 882.9 N (90 kg $\times$ 9.81 m s^{-2}) against the Earth upon which it stands. An object held in your hand exerts a force against your hand, which results from the object's mass and gravity's pull. Release the object, and the acceleration from gravity's effects becomes apparent as the object picks up speed as it falls to Earth (figure 4.27). Gravity's persistent attempt to accelerate a terrestrial animal downward constitutes the animal's weight. In tetrapods, this is resisted by the limbs.

The weight of a quadrupedal animal is distributed among its four legs. The force borne by fore- and hindlimbs depends on the distance of each from the center of the animal's mass. Thus, a large *Diplodocus* might have distributed its 18 metric tons (39,600 pounds) with a ratio of 4 tons to its forelimbs and 14 to its hindlimbs (figure 4.28).

When we explored the consequences of size and mass at the beginning of this chapter, we noted that large animals have relatively more mass to contend with than small

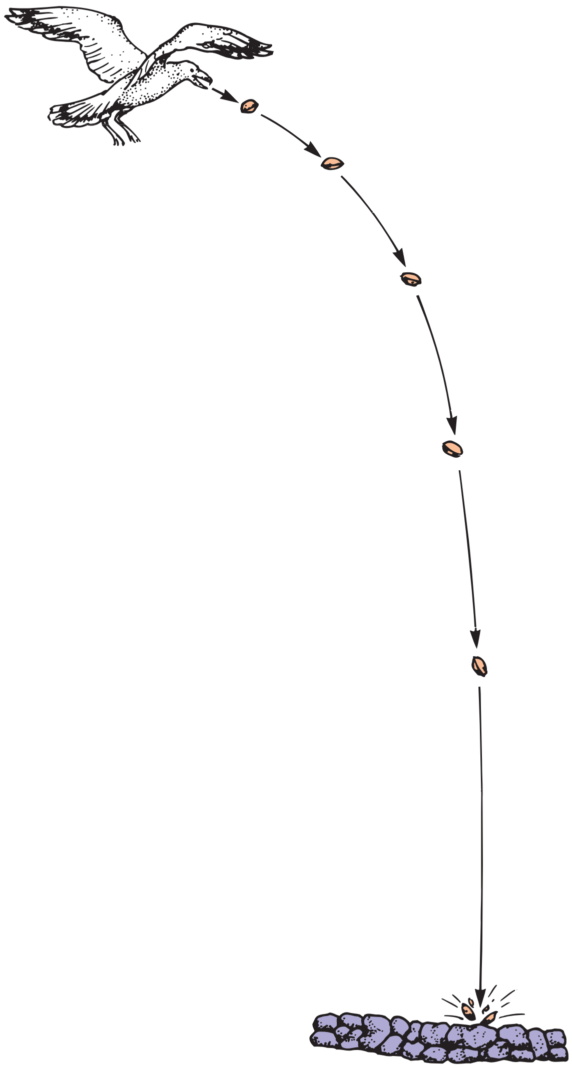


FIGURE 4.27 Gravity. The clam released by the seagull accelerates under gravity's pull and picks up speed as it falls to the rocks. With equal intervals of time designated by each of the six arrows, note the accelerating positions of the clam.

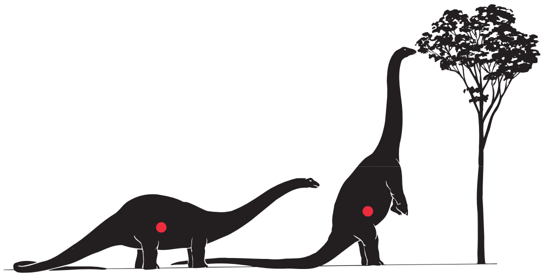


FIGURE 4.28 Weight distribution. (a) The estimated center of mass of this dinosaur lies closer to the hindlimbs than to its forelimbs, so the hindlimbs bear most of the animal's weight. For *Diplodocus,* its 18 metric tons (39,600 pounds) might have been carried by a ratio of 4 tons to its forelimbs and 14 tons to its hindlimbs. (b) If *Diplodocus* lifted its head and forefeet up to reach high vegetation, then all 18 tons would have been carried by hindlimbs and tail, which, forming three points of support, give each limb and the tail 6 tons to carry.

animals. A small lizard scampers safely across tree limbs and vertical walls; a large lizard is earthbound. Gravity, like other forces, is a part of an animal's environment and affects performance in proportion to body size. Size is also a factor for animals that live in fluids, although forces other than gravity tend to be predominant.

Life in Fluids

Dynamic Fluids Water and air are fluids. Air is certainly thinner and less viscous than water, but it is a fluid nonetheless. The physical phenomena that act on fishes in water generally apply to birds in air. Air and water differ in viscosity, but they place similar physical demands on animal designs. When a body moves through a fluid, the fluid exerts a resisting force in the opposite direction to the body's motion. This resisting force, termed **drag,** may arise from various physical phenomena, but forces caused by **friction drag** (or skin friction) and by **pressure drag** (see below) are usually the most important. As an animal moves through a fluid, the fluid flows along the sides of its body. As fluid and body surface move past each other, the fluid exerts a resisting force (drag) on the surface of the animal where they make contact. This force creates friction drag and depends, among other things, on the viscosity of the fluid, the area of the surface, the surface texture, and the relative speed of fluid and surface.

Individual particles in a fluid traveling in a flow describe individual paths. If the average direction of these particles is plotted and points connected along the line of overall flow, nonoverlapping streamlines that represent the general layered pattern of fluid flow are produced. The derived **streamlines** therefore express the statistical summary of layered flows slipping smoothly across one another within a moving fluid. Special and often complex events occur within the **boundary layer,** the thin, fluid layer closest to the surface of the body. Generally it is a thin gradient slowing from the velocity of the general flow down to zero on the surface of the object across which the fluid flows. In your car traveling at 60 mph (96 kmh), the air velocity drops from 60 mph down to zero in the boundary layer, which is one reason clinging insects on your windshield in this boundary layer can hold on. This layer can be very thin. In a Boeing 747, the boundary layer is about 1 in. thick at the trailing edge of the wing. Natural instabilities in the boundary layer may cause the fluid to become chaotic and the flow is spoken of as turbulent. This increases drag dramatically. Where the flow is smooth and nonchaotic, it is described as laminar.

If the particles in the boundary layer passing around an object are unable to make the sharp turn smoothly behind the object, then the layers within the flow tend to part; this is termed **flow separation** (figure 4.29a). The fluid behind the object moves faster and pressure drops leading to pressure drag, which may be seen as a wake of disturbed fluid behind

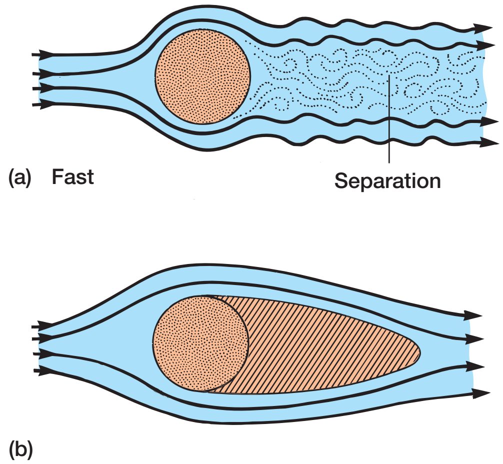


FIGURE 4.29 Streamlining. (a) Particles in the boundary layer are unable to make the sharp change in direction and velocity to negotiate the turn around the cylinder-shaped object, and flow separation occurs behind the object. (b) Extension and tapering of the object into the area of disturbance helps prevent separation and results in a streamline shape.

a boat. Physically, the flow separation results from a substantial pressure differential (pressure drag) between the front and the back of the animal. An extended, tapering body fills in the area of potential separation, encourages streamlines to close smoothly behind it, and thereby reduces pressure drag (figure 4.29b). The result is a streamlined shape common to all bodies that must pass rapidly and efficiently through a fluid. An active fish, a fast-flying bird, and a supersonic aircraft are all streamlined for much the same reason—to reduce pressure drag (figure 4.30a–d).

A golf ball in flight meets the same problems but is engineered differently to address drag forces. The dimpled surface of a golf ball helps hold the boundary layer longer, smoothes the streamlines, reduces the size of the disturbed wake, and, hence, reduces pressure drag. As a result, a golf ball with dimples travels, other things being equal, about twice as far as one with a smooth surface.

Together, friction and pressure drag contribute to **profile drag,** which is related to the profile or shape an object presents to the moving fluid. If you place your cupped hand out the window of a fast-moving car, you can feel the difference when presented edge-on or palm-on to the onrushing air. A change in profile changes the drag. A thin, broad wing of a bird meeting the air edge-on presents a small profile. But as the wing tips up, changing the angle of attack, the broad profile of the wing meets the air, increasing drag. Fish fins or seal flippers, when used to make sharp turns, are moved with the broadest profile to the water, much like the power stroke of a boat oar, taking advantage of profile drag to help generate cornering forces.

Engineers examine the physical problems associated with motion through fluids within the disciplines of hydrodynamics (water) or aerodynamics (air). Applied to animal designs that move through fluids, these disciplines reveal how size and shape affect the way the physical forces of a fluid act on a moving body.

In general, four physical characteristics affect how the fluid and body dynamically interact. One of these is the *density,* or mass per unit volume of the fluid. A second is the *size* and *shape* of the body as it meets the fluid. The resistance a rowboat oar experiences when the blade is pulled broadside-on is, of course, quite different than when it is pulled edge-on. The third physical characteristic of a fluid is its *velocity.* Finally, the *viscosity* of a fluid refers to its resistance to flow. These four characteristics are brought together in a ratio known as the Reynolds number:

$$Re = \frac{\rho l U}{\mu}$$

where ρ is the density of the fluid and μ is a measure of its viscosity; l is an expression of the body's characteristic shape and size; and U is its velocity through the fluid.

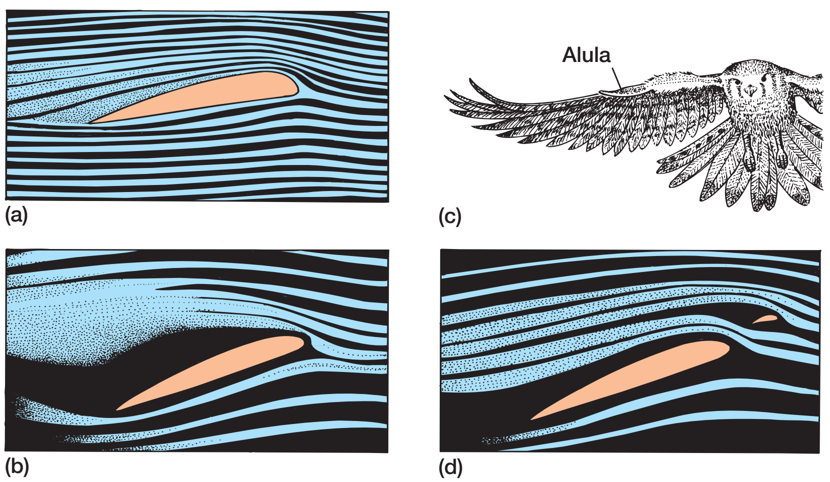


FIGURE 4.30 Life in fluids. (a) The airplane wing, shown in cross section, encourages smooth flow of the passing airstream. (b) As the angle of the wing increases relative to air flow, separation of flow from the upper wing surface suddenly forms and lift is lost. (c) Birds, such as this falcon, have a small tuft of feathers (alula) that can be lifted to smooth the airflow at high angles of attack. (d) When separation begins, this small airfoil can be lifted to form a slot that accelerates air over the top of the wing, preventing separation and thus stalling—a sudden drop in lift.

Modified from McMahon and Bonner.

Perhaps because we ourselves are large land vertebrates, we have some intuition about the importance of gravity but no special feeling for all that the Reynolds number has to tell us about life in fluids. The units of all variables of the ratio cancel each other, leaving the Reynolds number without units—no feet per second, no kilograms per meter, nothing. It is dimensionless, a further factor obscuring its message; yet, it is one of the most important expressions that summarizes the physical demands placed upon a body in a fluid. The Reynolds number was developed during the nineteenth century to describe the nature of fluid flow, in particular, how different circumstances might result in fluid flows that are dynamically similar. The Reynolds number tells us how properties of an animal affect fluid flow around it. In general, at low Reynolds numbers, skin friction is of great importance; at high Reynolds numbers, pressure drag might predominate. Perhaps most importantly, at least for a biologist, the Reynolds number tells us how changes in size and shape might affect the physical performance of an animal traveling in a fluid. It draws our attention to the features of the fluid (viscosity) and the features of the body (size, shape, velocity) that are most likely to affect performance.

For scientists performing experiments, the Reynolds number helps them to build a scale model that is dynamically similar to the original. For example, several biologists wished to examine air ventilation through prairie dog burrows but lacked the convenient space to build a life-sized tunnel system in the laboratory. Instead, they built a tunnel system ten times smaller but compensated by running winds ten times faster through it. The biologists were confident that the scale model duplicated conditions in the full-sized original because a similar Reynolds number for each tunnel verified that they were dynamically similar even though their sizes differed.

Static Fluids Fluids, even thin, low-density fluids such as air, exert a pressure on objects within them. The unit of pressure, Pascal (Pa), is equivalent to 1 newton acting over 1 square meter. The expression "as light as air" betrays the common misconception that air has almost no physical presence. In fact, air exerts a pressure in all directions of about 101,000 Pa (14.7 psi, or pounds per square inch) at sea level, which is equivalent to 1 **atmosphere** (atm) of pressure. The envelope of air surrounding Earth extends up to several hundred kilometers. Although not dense, the column of air above the surface of Earth is quite high, so the additive weight at its base produces a substantial pressure at Earth's surface. We and other terrestrial animals are unaware of this pressure since it comes from all directions and is counterbalanced by an equal outward pressure from our bodies. Thus, all forces on our bodies balance, inside with out. Respiratory systems need only produce relatively small changes in pressure to move air in and out of the lungs.

If we drive from low elevation to high elevation in a short period of time, we might notice the unbalanced pressure that builds uncomfortably in our ears until a yawn or stretch of our jaw "pops" and equilibrates the inside and outside pressures to relieve the mismatch. Most of us have experienced increasing pressure as we dive deeper in water. At a given depth, the pressure surrounding an animal in water is the same from all sides. The deeper the animal, the greater is the pressure. In fresh water, with each meter of depth, atmospheric pressure increases by about 9.8×10^3 Pa. At 5 meters, atmospheric pressure would be about 49×10^3 Pa. Scaled for a human, that would be like trying to breathe with a 90-kg slab placed upon the chest. A fully submerged sauropod would experience 49×10^3 N on each square meter of its entire chest (figure 4.31). It is not likely that even the massive chest muscles of this dinosaur could overcome so much pressure when it drew in a breath. Therefore, *Brachiosaurus* and other long-necked animals probably did not live aquatic lives with their bodies deeply submerged and their heads reaching far above to the surface to snorkel air. Snorkeling works only for small creatures close to the water's surface such as mosquito larvae or a blow-hole-equipped cetacean breaching the surface.

Buoyancy describes the tendency of a submerged object in a fluid to sink or to rise. Long ago, Archimedes (287–212 B.C.E.) figured out that buoyancy was related to the *volume* an object displaces compared to its own weight.

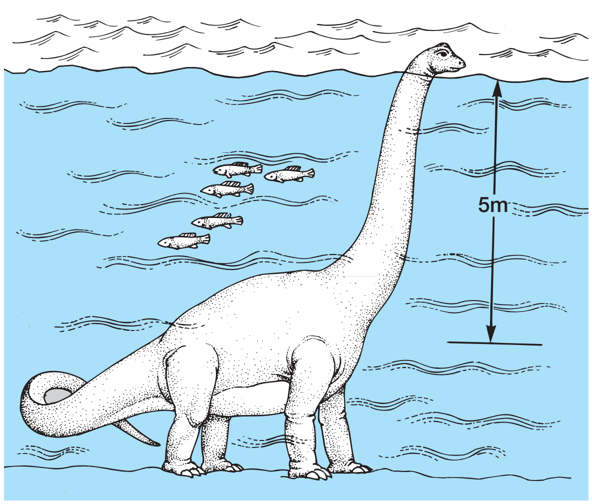


FIGURE 4.31 Water pressure. Water pressure increases with depth, but at any given depth, pressure is equal from all directions. For each meter below the surface, the pressure in fresh water increases by about 9,800 Pa. A large sauropod submerged up to its chin would experience water pressure of about 49,000 Pa (5 m $\times$ 9,800 Pa) around its chest, too much pressure to allow chest expansion against this force. Breathing would be impossible. Sauropods such as *Brachiosaurus* were probably not so completely aquatic as shown here, and certainly they would not have used a tall neck to snorkel air well above their submerged chest.

If the density of the submerged object is less than that of water, then buoyancy will be a positive upward force; if its density is greater than water, then the buoyancy is negative and it is forced down. Since density is related to volume, any change in volume will affect the tendency of the object to rise or sink. Many bony fishes possess a flexible gas bladder (swim bladder) that can be filled with various gases. As the fish dives deeper, pressure increases, compressing the air, reducing volume, and thereby effectively making the fish denser. The negative buoyancy now pushes the fish down, and it starts to sink. As we will see in chapter 11, such a fish can add more gas into the gas bladder to increase its volume and return it, overall, to neutral buoyancy.

Machines

When we are interested in the motions of parts of the same animal, it is customary to represent each movable part with a link. A joined series of links is a **kinematic chain** representing the main elements of an animal. If these linkages are floppy and without control, then the chain is said to be unconstrained. A kinematic chain restricted in motion is constrained and formally constitutes a **mechanism.** The motion of one link will impart a definite and predictable motion in all other links of the same mechanism (figure 4.32a).

A kinematic mechanism simulates the relative motions of the parts of the animal it represents, so it helps identify the role of each element. For example, several bony elements on both sides of a lizard's skull are involved when it lifts its snout during feeding. These elements can be represented by a kinematic chain that constitutes the jaw mechanism of the lizard (figure 4.32b, c).

Often we are interested in more than just the motion of a mechanism. We might want to know something about the transfer of actual forces. Such devices that transfer forces are **machines.** Formally defined, a machine is a mechanism for transferring or applying forces. In a car's engine, the pistons transfer the explosive forces of gasoline combustion to the connecting rod, the rod to the crankshaft, and the crankshaft in turn to the gears, axles, and wheels. Pistons to wheels collectively form a "machine" that transfers energy from the ignited gasoline to the road. Levers that transfer forces qualify as machines too. The input force brought into a machine by a lever arm is applied elsewhere as an output force by the opposite lever arm. In this engineering sense, the jaws of a herbivore are a machine whereby the input force produced by the jaw muscles is transferred along the mandible as an output force to the crushing molar teeth (figure 4.33).

Strength of Materials

A weight-bearing structure carries or resists the forces applied to it. These forces, termed a **load,** can be experienced in three general ways. Forces pressing down on an object to compact it are **compressive forces,** those that stretch it are **tensile forces,** and those that slide its sections are **shear forces** (figure 4.34a–c). Surprisingly, the same structure is not able to withstand the three types of force applications equally. For any structure, the maximum force a structure sustains in compression before breaking is its **compressive strength;** in tension, is its **tensile strength;** and in shear, is its **shear strength.** Internal forces, termed **stress,** are the reaction to these external forces loaded on the structure.

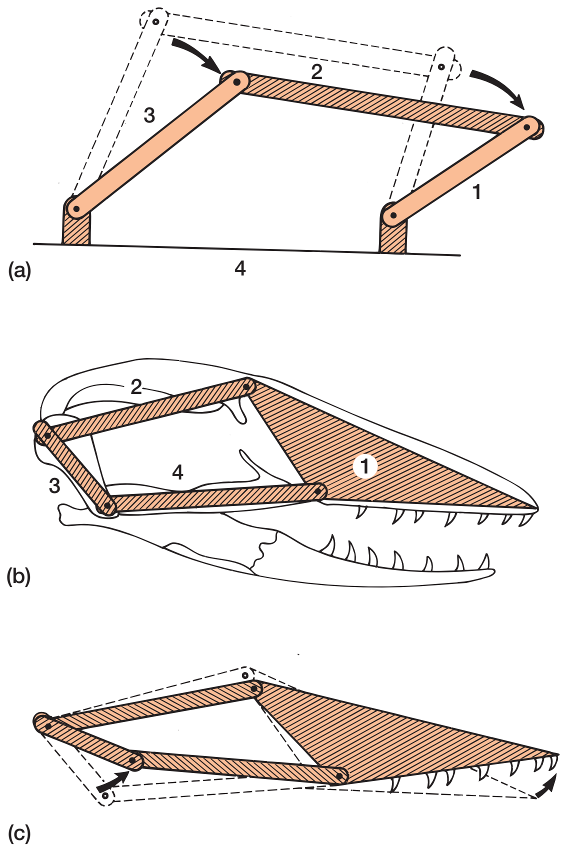


FIGURE 4.32 Kinematic chain. (a) This four-linkage mechanism is joined by pin connections so that the motion of link 3 imparts a specific motion to the three other links. (b) The four-linkage chain of a lizard skull (ignoring the lower jaw) is constrained. (c) Again, motion of link 3 imparts a specific motion to each of the other links. After T. H. Frazzetta

Table 4.2 lists the strengths of several materials when they are exposed to compressive, tensile, and shear forces. Notice from this table that most materials are strongest in resisting compressive forces and weakest in their ability to withstand tension or shear. This is very significant in design. Ordinarily, supportive columns of buildings bear the load in a compressive fashion, their strongest weight-bearing orientation. However, if the column bends slightly, tensile forces, to which they are more susceptible, appear.

When any object bends, compressive forces build up on the inside of the bend and tensile forces on the outside. Opposite sides experience different force applications. The column may be strong enough to withstand compressive forces, but the appearance of tensile forces introduces forces it is intrinsically weaker in resisting. If bending persists, breaks may originate on the side experiencing tension, propagate through the material, and cause the column to fail. Flying buttresses, side braces on the main support piers (columns) of Gothic cathedrals, were used to prevent the piers from bending, thus keeping them in compression and allowing them to better carry the weight of the cathedral's arched roof (figure 4.35).

Loads

How a load is positioned upon a supportive column affects its tendency to bend (figure 4.36a–c). When the load is arranged evenly above the column's main axis, no buckling is induced and the column primarily experiences the load as compressive force (figure 4.36b). The same load placed asymmetrically off center causes the column to bend (figure 4.36c). Tensile (and shear) forces now appear. Tensile and compressive forces are greatest at the surfaces of the column, least at its center. Development of surface tensile forces is especially ominous because of the intrinsic susceptibility of supportive elements to such forces—what we notice as cracks.

Biological Design and Biological Failure

Fatigue Fracture With prolonged or heavy use, bones, like machines, can fatigue and break. When initially designed, the working parts of a machine are built with materials strong enough to withstand the calculated stresses they will experience. However, with use over time, these parts often fail, a

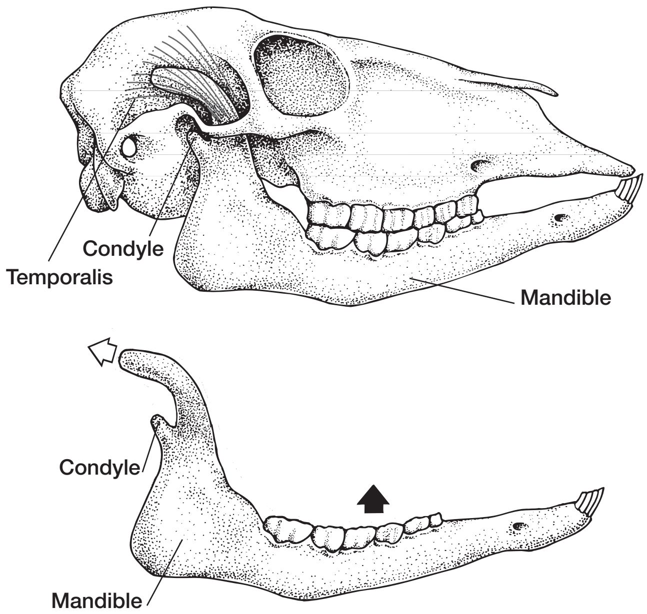


FIGURE 4.33 **Jaws as machines.** A machine transfers forces. Here the lower jaw of a herbivore transfers the force of the temporalis muscle (open arrow) to the tooth row (solid arrow) where food is chewed. Rotation occurs about the condyle.

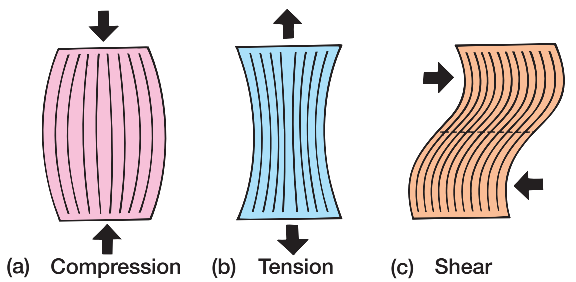


FIGURE 4.34 **Direction of force application.** The susceptibility of a material to breaking depends on the direction in which the force is applied (arrows). Most materials withstand compression best (a) and are weaker when placed in tension (b) or shear (c).

TABLE 4.2 Strength of Different Materials Exposed to Compressive, Tensile, and Shear Forces

Material	Compressive Strength (Pa)	Tensile Strength (Pa)	Shear Strength (Pa)
Bone	165×10^6	110×10^6	65×10^6
Cartilage	27.6×10^6	3.0×10^6	0.26×10^6
Concrete	24.1×10^6	4.0×10^6	1.6×10^6
Cast iron	620.5×10^6	310.2×10^6	379.2×10^6
Granite	103×10^6	10×10^6	13.8×10^6

Ultimate strengths shown.

Source: Adapted from J. E. Gordon, 1978. Structures, or why things don't fall down, *DaCapo Press, NY. Other sources have also been used.*

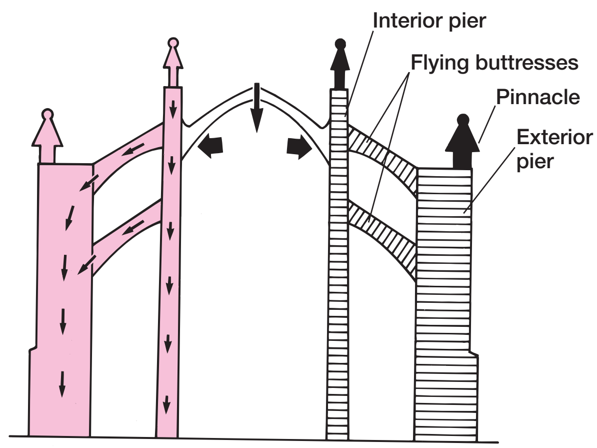


FIGURE 4.35 **Gothic cathedral.** The right side of the cathedral shows its structural elements. The left side illustrates how these structures carry the thrust lines of forces. At its simplest, the cathedral includes the exterior pier topped by a pinnacle, the main interior pier, and the flying buttresses between the interior and exterior piers. The weight of the vault (roof) produces an oblique thrust against the interior piers. Wind pressure or snow load accentuates this lateral pressure, which tends to bend the main interior piers. Flying buttresses act in an opposite direction to resist this bending and help carry lateral thrust from the roof to the ground (small arrows).

After Gordon.

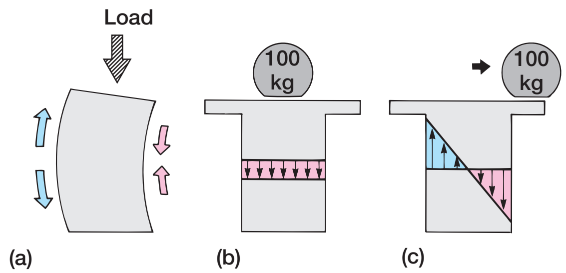


FIGURE 4.36 Loading. (a) When a material bends under a load, compressive forces (solid arrows) develop along the concave side, tensile forces (open arrows) along the convex side. (b) When a supportive column is loaded symmetrically (with the weight centered), the only type of force experienced is compressive force. The distribution of the 100-kg mass within a representative section is depicted graphically. The lengths of the down arrows show equal distribution of compressive forces within this representative section. (c) Asymmetrical loading of the same mass causes the column to bend. The column experiences compressive forces (down arrows) and tensile forces (up arrows). Both compressive and tensile forces are greatest near the surface and least toward the center of the column.

condition known to engineers as **fatigue fracture.** Not long after the Industrial Revolution, engineers noticed that moving parts of machinery occasionally broke at loads within safe limits. Axles of trains, in use for some time, suddenly broke for no apparent reason. Cranks or cams that had withstood peak loads many times before sometimes suddenly broke under routine operation. Eventually engineers appreciated that one of the factors leading to these failures was fatigue fracture. Although a moving part might be strong enough initially to bear up easily to peak loads, over time tiny microfractures form in the material. These are insignificant individually, but cumulatively they can add up to a major fracture that exceeds the strength of the material, and breakage follows.

Load Fracture In vertebrates, bones are loaded symmetrically or, where that is not possible, muscles and tendons act as braces to reduce the tendency for a load to induce bending of a bone (figure 4.37). The greatest stresses develop at the surface of bone, while forces are almost negligible at its center. Consequently, the core of a bone can be hollow without much loss of its effective strength. Probably for the same reason, cattail reeds, bamboos, bicycle frames, and fishing poles are hollow as well. This economizes on material without a great loss in strength.

Most fractures likely begin on the side of the bone experiencing tensile forces. To start it, a fracture requires energy as intermolecular bonds begin to break, but as it propagates, more energy is released than is consumed so the fracture tends to grow easily and quickly. Think for instance of tearing a piece of paper—the tear starts with some effort but rips (fractures) more easily once underway. In bone, a fracture propagates through the matrix, causing failure. Bone, however, is a composite material consisting of several substances with different mechanical properties. Together these substances resist the propagation of a fracture better than any one constituent alone (figure 4.38a–c). This same principle of composites gives fiberglass its resistance to breaking. Fiberglass consists of glass fibers embedded in a plastic resin. Glass is brittle, resin weak, but together they are strong because they blunt small cracks and prevent their spread. As a crack approaches the boundary between the two fiberglass materials, the resin gives slightly. That spreads out

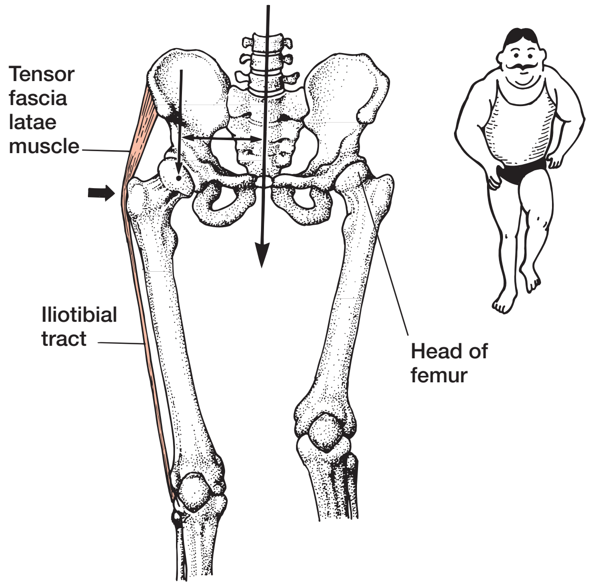


FIGURE 4.37 Braces. The weight of the upper body is carried on the heads of the femurs (left). This means that during the striding gait (right), the head of one femur carries all the upper body weight. Consequently, the long shaft of the femur is loaded asymmetrically, increasing its tendency to bend. The iliotibial tract, the long tendon of the tensor fasciae latae muscle that runs laterally across the femur, partially counteracts this tendency to bend and thereby reduces the tensile forces that would otherwise develop within the femur.

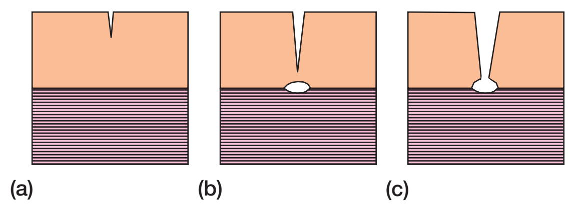


FIGURE 4.38 Fracture propagation. (a) Failure of a structure begins with the appearance of a microfracture that spreads rapidly. (b) In composite materials, such as bone, the advancing fracture is preceded by stress waves that may cause the concentrated force to spread at the boundary between the composite materials, where they give slightly. (c) As the fracture line meets this boundary, its sharp tip is blunted and its progress curtailed.

the force and thus reduces the stress at the tip of the crack that makes it advance. A space in the material can do the same job; thus hard foams resist cracking. Bone makes use of both stress relief and small voids or spaces to reduce crack propagation.

Collagen fibers and hydroxyapatite crystals are the main materials of bone matrix. They are thought to act in a manner analogous to the glass and resin of fiberglass to blunt small fractures. Further, the orientation of collagen fibers alternates in successive layers so that they better receive tensile and compressive forces.

Teeth, too, seem to be built to stop cracks. The outer part of a tooth is enamel, the inner part dentin. Enamel is almost pure ceramic, a calcium phosphate mineral called hydroxyapatite; but dentin, in addition to hydroxyapatite, also includes about 40% of the protein collagen. The result—enamel and dentin have different physical properties. When a microcrack propagates through the enamel toward dentin at the tooth interior, it stops at the boundary with the dentin. At this enamel-dentin interface, the surface is scalloped, which deflects the trajectory of the arriving crack, decreasing its full force, and thereby serves to stop the crack's spread.

Bone structure (p. 182); tooth anatomy (p. 507)

Tissue Response to Mechanical Stress

Tissues can change in response to mechanical stress. If living tissue is unstressed, it tends to decrease in prominence, a condition termed **atrophy** (figure 4.39a). If it experiences increased stress, tissue tends to increase in prominence, a condition termed **hypertrophy** (figure 4.39b). Cell division and proliferation under stress are termed **hyperplasia.** Thus, in response to exercise, the muscles of an athlete will increase in size. This overall increase is primarily due to an increase in the size of existing muscle cells, not to an increase in cell

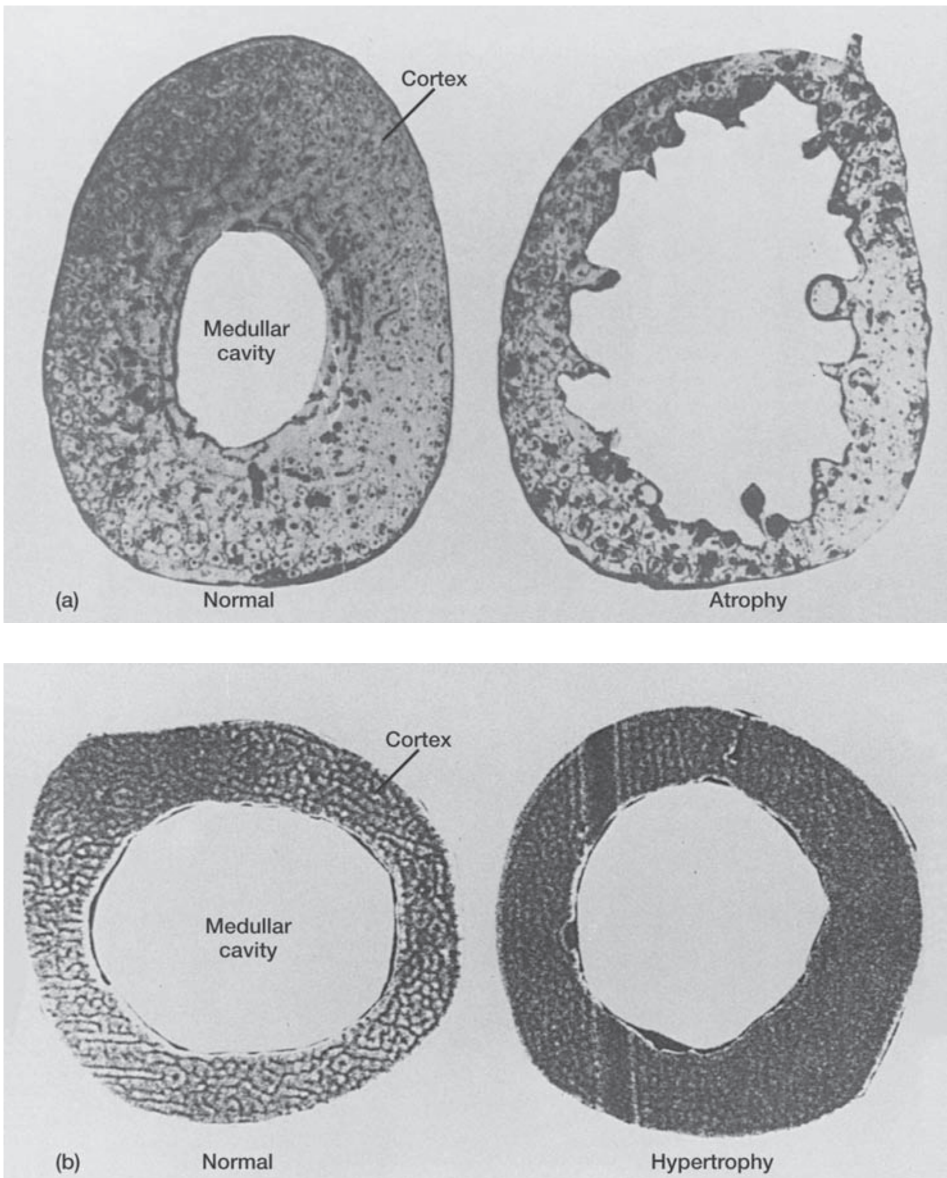


FIGURE 4.39 Loss (atrophy) and increase (hypertrophy) of bone. (a) Cross section of a normal foot bone from a dog is illustrated on the left. Cross section of the same bone from the opposite foot (right) that was immobilized in a cast for 40 weeks reveals significant atrophy. (b) Cross section of a normal femur from a pig is depicted on the left. Cross section of a femur from a pig that had been vigorously exercised on a regular basis for over a year shows increased bone mass (right). Hypertrophy is evident from the thickening and greater density of the bone cortex.

number (hypertrophy but not much hyperplasia). During pregnancy, smooth muscles of the uterus increase both in size and number (hypertrophy and hyperplasia).

Muscle response to chronic exercise (p. 382)

Tissues can, under some circumstances, change from one type to another, a transformation called **metaplasia.** Metaplastic transformations are often pathological. For example, the normal ciliated pseudostratified columnar epithelium of the trachea may become stratified squamous epithelium in tobacco smokers. But some metaplastic changes seem to be part of normal growth and repair processes as well. For example, reptiles exhibit metaplastic bone formation during growth of long bones. Chondrocytes become osteoblasts and cartilaginous matrix becomes osseous as cartilage undergoes direct transformation into ossified bone. During bone repair in reptiles, amphibians, and fishes, the cartilaginous callus appears to arise from connective tissue through metaplasia.

Tissue types (p. 177)

All tissues retain some physiological ability to adjust to new demands, even after embryonic development is complete. Weight training causes an athlete's existing muscles to increase and his or her tendons to strengthen. Regular long distance running enhances circulation, increases blood volume, improves oxygen delivery to tissues, and metabolizes stored lipids more efficiently. Although the number of nerve cells does not usually increase in response to the physiological stress of exercise, coordination of muscle performance often does. Tissues continue to adapt physiologically to changes in demand throughout the life of the individual. One of the best examples is bone because it illustrates the complexity of tissue response.

Responsiveness of Bone

While performing in a protective or supportive role, bone cannot significantly deform or change shape. Leg bones that telescope or bend like reeds would certainly be ineffective as supports for the body. Bones must be firm. But because living bone is dynamic and responsive, it gradually changes during the life of an individual. The genetic program of a person sets forth the basic form a bone takes, but immediate environmental factors also contribute to ultimate bone form. Some peoples of the New World developed the practice of wrapping a baby's head against a cradle board (figure 4.40a, left). As a result, the normal skull shape of the baby was altered so that the side pressed to the board was flattened. In parts of Africa and Peru, prolonged bandaging of the back of the skull caused elongation of the cranium (figure 4.40a, right). Until recent times, young Chinese girls who looked forward to a leisured life had their feet permanently folded and tightly bound to produce tiny feet in adulthood. The toes were crowded and the arch exaggerated (figure 4.40b, right). The normal and, by comparison, large foot was considered ugly in women (figure 4.40b, left). Because foot-binding

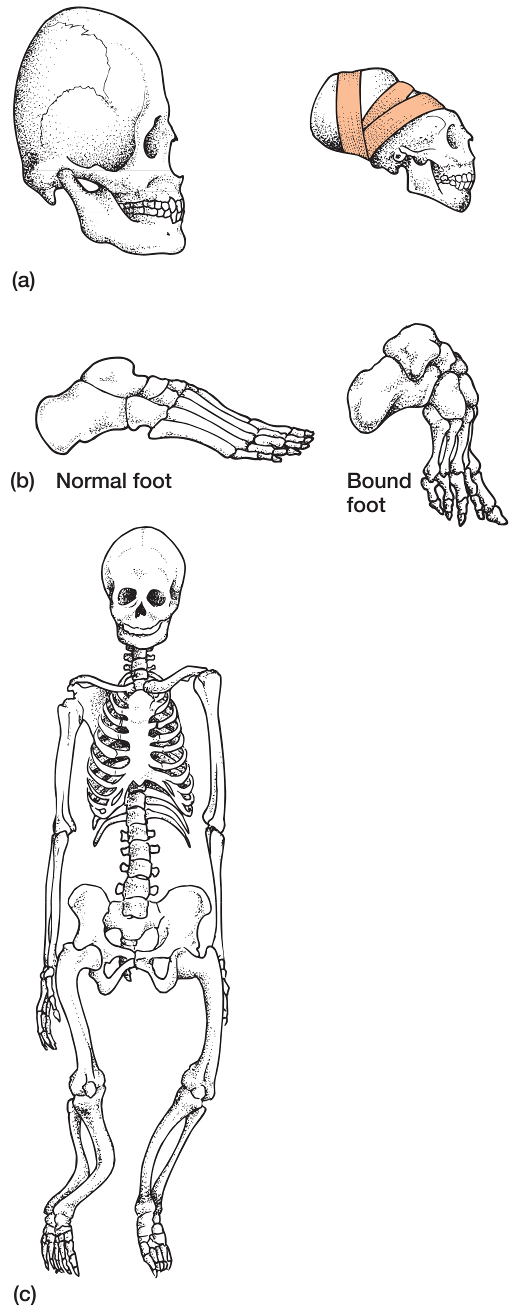


FIGURE 4.40 Responsiveness of bone to mechanical stress. (a) The continuous mechanical pressure of a cradle board flattened the back of the Navajo Indian skull (left), and wrapping of the Peruvian native skull (right) caused it to elongate. (b) Historically, many Chinese followed the practice of binding the feet of young girls with tight wrappings. The small, deformed foot shown on the right was considered socially "attractive." (c) A nutritional calcium deficiency during infancy led to rickets, which weakened this woman's skeleton, shown here at age 70. Her bones bent under the normal load of her body.

After Halsted and Middleton.

BOX ESSAY 4.1 Repairing Damaged Bone—Heal Thyself

When bone sustains prolonged stress, microdamage occurs in the form of microfractures. The response of bone is to physiologically adapt by mending these microfractures. The forelimb of tetrapods includes two bones (ulna, radius) we will meet in detail later, but for now we need only recognize that each mechanically buttresses the other. Remove one of these two bones and the other now, without its partner, experiences increased stress up to four times greater. However, after a few months these stresses decline and return to normal. What happens? The bone physiologically adjusts by laying down new bone to address the new stresses. The overload causes an increase in microdamage, which stimulates an increase in repair rate of new bone formation, remodeling it. This in turn reduces surface stress, which returns the bone's mechanical challenges to where it was before being damaged. At a genetic level, the changes in mechanical load stimulate important genes involved in bone formation. Think of it. Mechanical events reach into the bone cells and activate genes that produce not just new bone, but bone in the right places to address the new mechanical stresses. This is a wonderful insight. Consider the comments of one scientist. In older humans who fall and experience a hip fracture, over half may never live independently again and 20% are dead in half a year. Grim statistics. But now that the linkages from mechanical events to gene action are understood, there is promise.

impaired biomechanical performance, this also had what was considered the proper social consequence of keeping women literally "in their place."

Environmental Influences Four types of environmental influences alter or enhance the basic shape of bone set down by the genetic program. One is infectious disease. A pathogenic organism can act directly to alter the pattern of bone deposition and change its overall appearance. Or, the pathogen can physically destroy regions of a bone. A second environmental influence is nutrition. With adequate diet, normal bone formation is usually taken for granted. If the diet is deficient, bones can suffer considerable abnormalities. Rickets, for example, caused by a deficiency of calcium in humans, results in buckling of weight-bearing bones (figure 4.40c). Ultraviolet radiation transforms dehydrocholesterol into vitamin D, which the human body needs to incorporate calcium into bones. Sunshine and supplements of milk are usually enough to prevent rickets. Hormones are the third factor that can affect bone form. Bone is a calcium reservoir, which is perhaps its oldest function. When demanded, some calcium is removed from bone matrix. Calcium drains occur during lactation when the female produces calcium-rich milk, during pregnancy when the fetal skeleton begins to ossify, during egg laying when hard shell is added, and during antler growth when the bony rack of antlers is developing.

Endocrine control of bone calcium (p. 596)

The fourth environmental influence on bone form is mechanical stress (figure 4.40b, c). Each weight-bearing bone experiences gravity, and muscles tug on most bones. Forces produced by gravity and muscle contraction place bone in an environment of stresses that determine the final shape of bone. Throughout an individual's life, these stresses upon bone change. As a young animal gains its footing and daring, it becomes more active. As an adult, it might migrate, battle for territory, or increase its foraging to support offspring of its own. As the animal grows bigger, scaling becomes a factor. Geometric increase in the mass of a growing animal places greater mechanical demands upon the supportive elements of its body. Human athletes on a continuous training program intentionally increase their loads on bones and muscles to stimulate physiological adaptation to the heightened activity. Conversely, age or inclination can lead to declining activity and reduced stress on bones. Teeth might decay, and this changes the stress pattern experienced by the jaws. An injury can lead to favoring one limb over another. For a variety of reasons, then, the forces experienced by bones change.

Atrophy and Hypertrophy The response of bone to mechanical stresses depends upon force duration. If bone experiences continuous pressure, bone tissue is lost and atrophy occurs. Continuous pressure against bone arises occasionally with abnormal growths, such as brain tumors that bulge from the surface of the brain and press on the underside of the bony skull. If this continuous pressure is prolonged, the bone erodes, forming a shallow depression along the surface of contact. Aneurysms, balloonings of blood vessels at weak spots in the vessel wall, can exert continuous pressure against nearby bone and cause it to atrophy. Orthodontic braces cinched to teeth by a dentist force teeth up against the sides of the bony sockets in which they sit. Resorption of continuously stressed bone opens the way for teeth to migrate slowly but steadily into new and presumably better positions within the jaws.

Thus, bone that experiences a continuous force atrophies; however, so does bone that experiences no force. When forces are absent, bone density actually thins. People restricted to prolonged bed rest without exercise show signs of osteoporosis. This has been studied experimentally in dogs on whom a cast has been applied to one leg. The immobilizing cast eliminates or considerably reduces the normal loads carried on a leg bone. Bones so immobilized exhibit significant signs of resorption, which can occur rather quickly. Experiments with immobilized wings of roosters show that within a few weeks wing bones become extensively osteoporetic. Rarification of bone matrix occurs in astronauts during extended periods of weightlessness. Calcium salts leave bones, circulate in the blood, and this excess is actually excreted. When astronauts return to Earth's gravitational forces, their skeletons gradually recover their former density. Even over long voyages, the ossified skeleton is not likely to disappear altogether, but it may fall to a genetically determined minimum. And, of course, muscle contractions maintain some regime of forces on bone. But during deep space travel lasting many months, bone atrophy can progress far enough to make return to Earth's gravity hazardous. Prevention of bone atrophy in space travel remains an unsolved problem.

Between continuously stressed and unstressed bone is the third type of force application, *intermittent* stress. Intermittent stress stimulates bone deposition, or hypertrophy. The importance of intermittent forces on bone growth and form has long been suspected from the fact that bone atrophies when intermittent forces are removed. Conversely, when rabbit bones were intermittently stressed by a special mechanical apparatus, hypertrophy occurred. More recently, bones of the rooster wing were stressed once daily with compressive loads but otherwise left immobilized. After a month, the artificially stressed bones did not exhibit osteoporosis but did show growth of new bone, clearly an appropriate physiological response to the artificially induced intermittent stresses.

Internal Design The overall shape of a bone reflects its role as part of the skeletal system. Internal bone tissue consists of areas of **compact bone** and **spongy bone.** Distribution of compact and spongy bone is also thought to be directed by mechanical factors, although there is little hard evidence to support this correlation. According to an engineering theory called the trajectorial theory, when a load is placed on an object, the material within the object carries the resulting internal stress along stress trajectories or paths that pass these forces from molecule to molecule within the object (figure 4.41a). A beam embedded at its base in the wall will bend under its own weight. The lower surface of the beam experiences compressive forces as the material is pushed together, and the upper surface of the beam experiences tension as material here is pulled apart. The resulting compressive and tensile stresses are carried along stress trajectories that cross at right angles to each other and bunch under the beam's surface.

Culmann and Meyer, nineteenth-century engineers, applied this trajectorial engineering theory to the internal architecture of bone. Because the femur carries the load or weight of the upper body, they reasoned that similar stress trajectories must arise within this bone. In order for the body to build a strong structure and yet be economical with material, bony tissue should be laid down along these stress trajectories, the lines along which the load is actually carried. After looking at sections of bone, Culmann suggested that nature arranged bone spicules **(trabeculae)** into a lattice of spongy bone at the ends of long bones (figure 4.41b). Because these lines of stress move to the surface near the middle of the bone, the trabeculae follow suit, and the overall result is a tubular bone. If the trabeculae of bone follow internal lines of stress, these trabeculae might be expected to form a lattice of spongy bone after birth when functional loads are first experienced. This is borne out. Trabeculae of young fetuses display random honeycomb architecture. Only later do they become arranged along presumed lines of internal stress.

Wolff's Law As applied mechanical forces change, bone responds dynamically to adapt physiologically to changing stresses. Wolff's Law, named for a nineteenth-century scientist who emphasized the relationship between bone form and function, states that remodeling of bone occurs in proportion to the mechanical demands placed upon it.

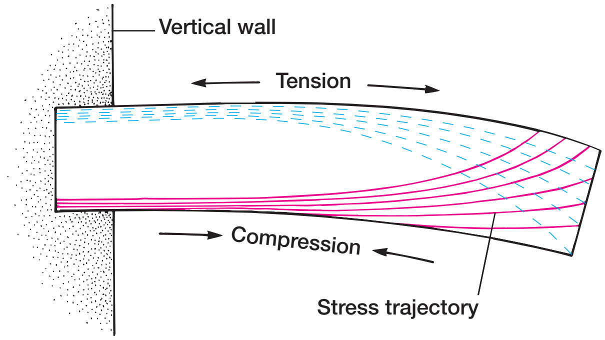
When bone experiences new loads, the result is often a greater tendency to buckle. When buckling occurs, tensile forces appear. Bones are less able to withstand tensile forces than they can compressive forces. In order to compensate, bone undergoes a physiological remodeling to better adapt to the new load (figure 4.42a–c). Initially, adaptive remodeling entails thickening along the wall experiencing compression. Eventually overall remodeling restores the even, tubular shape of the bone. How are cells along the compressive side selectively stimulated to deposit new bone? Nerves penetrate throughout bone, so they might be one way of promoting and coordinating the physiological response of osteocytes to changes in loading. However, bones to which nerves have been cut still abide by Wolff's Law and adjust to changes in mechanical demand.

Muscles pulling on bone affect the shape of vascular channels near their points of attachment to bone, which alters the blood pressure in vessels supplying bone cells. Increased muscle activity accompanying increased load might, via such blood pressure changes, stimulate bone cells to remodel. However, muscle action on bone, even if sufficient to change blood pressure, seems too global a mechanism to lead to the specific remodeling responses actually observed in bone.

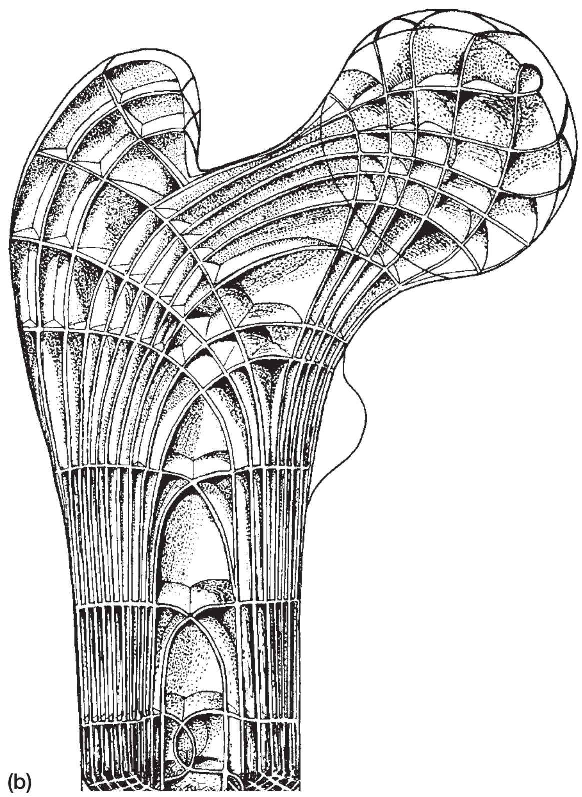
Bone cells occupy small lacunae, spaces within the calcium matrix of a bone. Slight configurational changes in the lacunae occupied by bone cells offer a more promising mechanism. Under compression, lacunae tend to flatten;

FIGURE 4.41 Stress trajectories. (a) A beam projecting from a wall tends to bend under its own weight, placing internal stresses on the material from which it is made. Engineers visualize these internal stresses as being carried along lines called stress trajectories. Compressive forces become concentrated along the bottom of the beam, tensile forces along the top. Both forces are greatest at the surface of the beam. (b) Stress trajectories in living bone. When this theory is applied to living bone, the matrix of bone appears to be arranged along the lines of internal stress. The result is an economical latticework of bone, with material concentrated at the surface of a tubular bone. A cross section through the proximal end of a femur reveals the lattice of bone spicules within the head that become concentrated and compacted along the wall within the shaft of the femur.

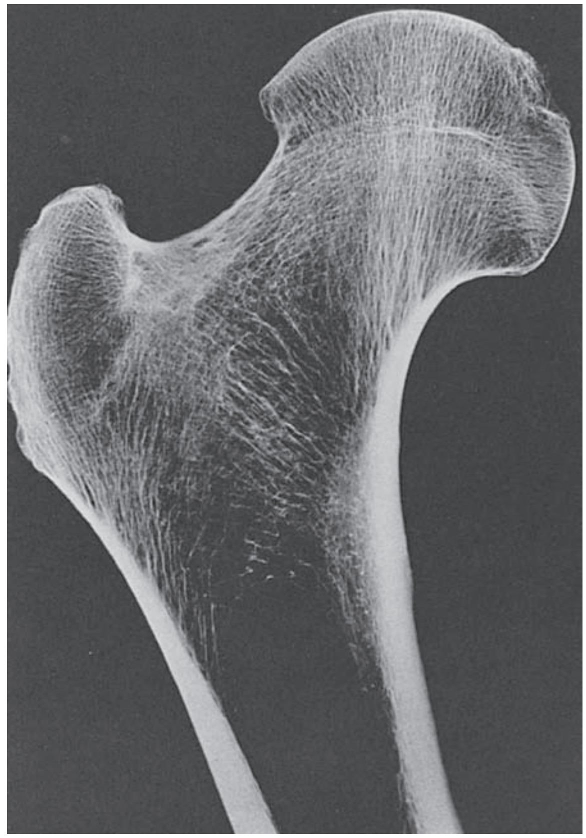
Latticework model kindly supplied by P. Dullemeijer, after Kummer.



(a)



(b)



under tension they tend to become round. If these configurational changes produced under load could be read by the bone cells occupying the lacunae, then bone cells might initiate a remodeling matched to the type of stress experienced.

Another mechanism might involve **piezoelectricity,** or low-level electric charges. These are surface charges that arise within any crystalline material under stress—negative charges appear on the surface under compression, and positive charges on the surface in tension. Bone, with its structure of hydroxyapatite crystals, experiences piezoelectric charges when it is loaded. It can be easily imagined that under a new load, a new environment of piezoelectric charges would appear within the tissue of stressed bone. If individual bone cells could key off these localized piezoelectric charges, then a specific remodeling response might follow.

Although promising, each of these proposed mechanisms by itself seems insufficient to account for the physiologically adaptive remodeling that occurs during bone response to the functional demands placed upon it. This is a challenging area for further research.

Biophysics and Other Physical Processes

Biophysics is concerned with principles of energy exchange and the significance of these principles for living organisms. The use of light, the exchange of heat, and the diffusion of molecules are fundamental to the survival of an organism. Biological design and its limits are determined by the

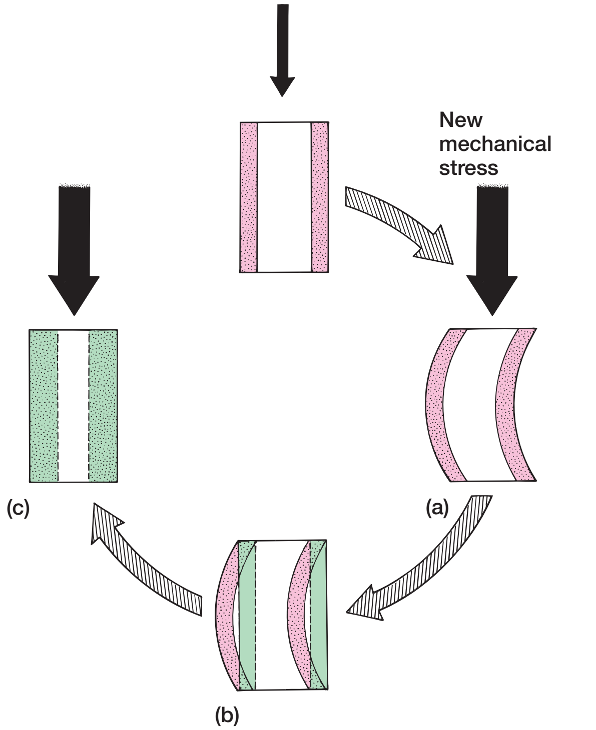


FIGURE 4.42 **Bone remodeling.** When tubular bone experiences a new and more distorting stress (a), it undergoes a physiological response that both thickens and straightens it. New bone forms along the concave surface (b), remodeling the bone, and the straight shape is restored (c). Further remodeling returns the bone to its original shape (top), although the walls would now be thicker to withstand the new, increased load.

physical principles governing energy exchange between an organism and its environment, and internally between active tissues within the organism. One of the most important of these physical principles applies to the exchange of gases.

Diffusion and Exchange

Pressures and Partial Pressures

Air pressure varies slightly with weather conditions, such as low- and high-pressure fronts, and with temperature. When animals ascend in altitude, air pressure drops significantly as the air thins (becomes less dense) and breathing becomes more labored. This drop in pressure of the gases, especially oxygen, creates the difficulty. Air is a mixture of nitrogen (about 78% by volume), oxygen (about 21% by volume), carbon dioxide, and trace elements. Each gas in air acts independently to produce its own pressure irrespective of the other gases in the mixture. Of the total 101,000 Pa (pressure of air) at sea level, oxygen contributes 21,210 Pa (101,000 Pa $\times$ 21%) to the total, nitrogen 78,780 Pa (101,000 Pa $\times$ 78%), and the remaining gases 1,010 Pa. Because each gas contributes only a part of the total pressure, its contribution is its **partial pressure.** The rate at which oxygen can be inhaled depends on its partial pressure. At 5,300 m (18,000 ft), air pressure drops to about 0.5 atm (atmosphere), or 50,500 Pa. Oxygen still composes about 21% of the air, but because the air is thinner, there is less total oxygen present. Its partial pressure falls to 10,605 Pa (50,500 Pa $\times$ 21%). With a drop in the partial pressure of oxygen, the respiratory system picks up less and breathing becomes more labored. Animals living in the high mountains, and especially high-flying birds, must be designed to address this change in atmospheric pressure.

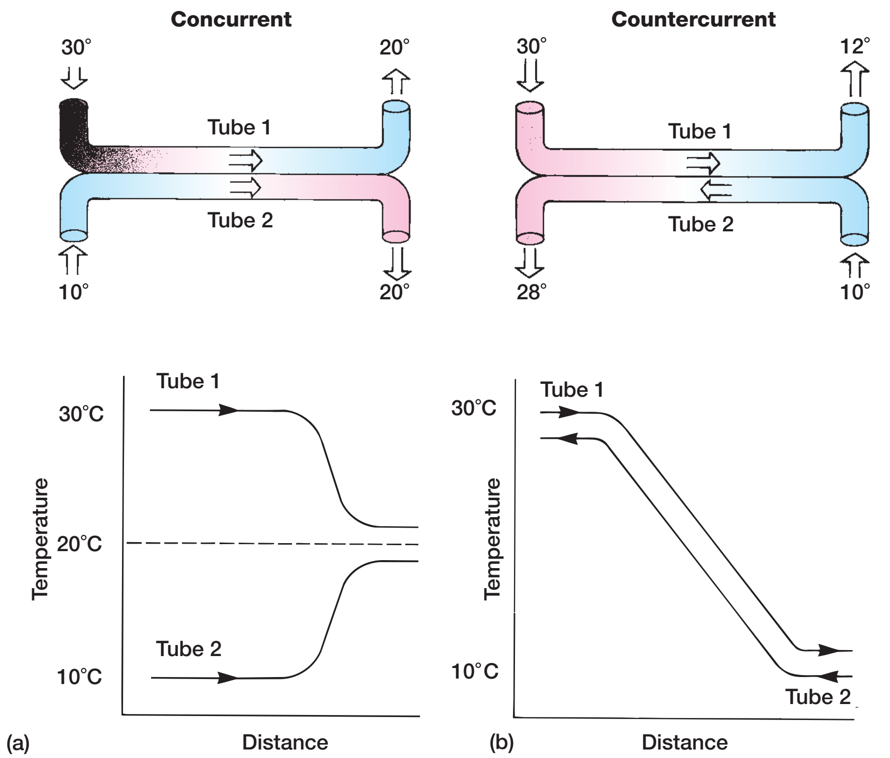
Because water weighs much more than air per unit of volume, an animal descending through water experiences pressure changes much more quickly than one descending through air. With each descent of about 10.3 m (33.8 ft), water pressure increases by about 1 atm. Thus, a seal at a depth of 20.6 m experiences almost two additional atmospheres of pressure more than it experiences when basking on the beach. The effect of this pressure change on body fluids and solids is probably inconsequential, but gas in the lungs or in the gas bladders of fishes is compressed significantly. Each 1-meter descent in water adds 9,800 Pa of pressure, or about 1.5 lb of pressure per square inch of chest wall. Compressing the lungs or the gas bladder reduces their volume and thus affects buoyancy. The movement of gases into and out of the bloodstream is affected by the difference in the partial pressure of oxygen breathed in at the surface and its partial pressure when it is diffused into the blood once the animal is submerged. We look specifically at these properties of gases and the way in which the vertebrate body is designed to accommodate them when we examine the respiratory and circulatory systems in chapters 11 and 12, respectively.

Countercurrent, Concurrent, and Crosscurrent Exchange

Exchange is a large part of life. Oxygen and carbon dioxide pass from the environment into the organism or from the organism into the environment. Chilled animals bask to pick up heat from their surroundings; large, active animals lose heat to their surroundings to prevent overheating. Ions are exchanged between the organism and its environment. This process of exchange, whether it involves gases, or heat, or ions is sometimes supplemented by air or water currents passing one another. Efficiency of exchange depends on whether the currents pass in opposite or equivalent directions.

Imagine two parallel, but separate, identical tubes through which streams of water flow at the same speed. Water entering one tube is hot, and water entering the other is cold. If the tubes are made of conducting material and contact each other, heat will pass from one to the other (figure 4.43a, b). Water flow may be in the same direction, as in **concurrent exchange,** or in opposite directions, as in **countercurrent exchange.** The efficiency of heat exchange between the tubes is affected by the directions of flow.

If the streams are concurrent, as the two tubes come in contact, the temperature difference will be at its maximum but will drop as heat is transferred from the hotter to



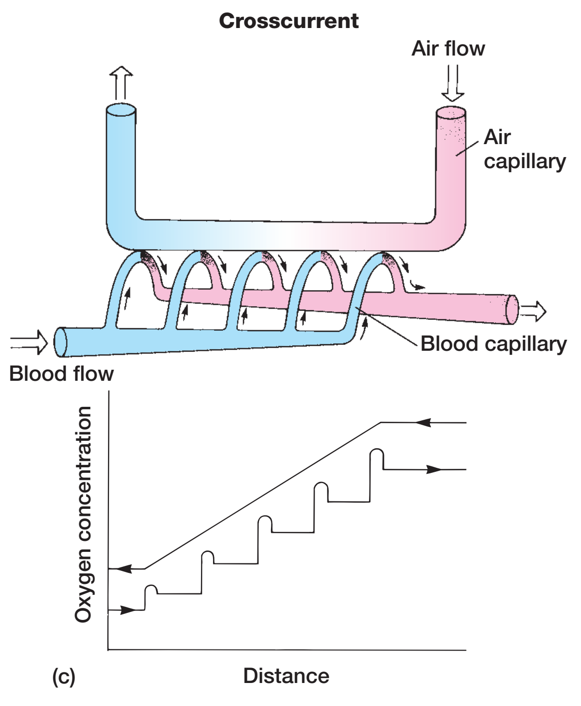


FIGURE 4.43 **Systems of exchange.** Direction and design of exchange tubes affect the efficiency of transfer regardless of whether the exchange involves heat, gases, ions, or other substances. The first two examples (a and b) illustrate heat transfer. The third example (c) depicts gas exchange. (a) Concurrent exchange describes the condition in which separated fluids flow in the same direction. Because the temperature gradient between the fluids is high when they enter the tubes and rather low when they exit, the average difference in heat exchanged between the two fluids is relatively high. The fluid in tube 2 is at 10° when it enters and at 20° when it exits. (b) In countercurrent exchange, the fluids pass in opposite directions within the two tubes so that the temperature difference between them remains relatively low all along their lengths. The fluid in tube 2 is at 10° when it enters and at 28° when it exits. Thus, more heat is transferred with countercurrent exchange than with concurrent exchange. (c) In a stepwise crosscurrent exchanger, each blood capillary branch passes across an air capillary at about right angles to it and picks up oxygen. The levels of oxygen rise serially in the departing blood. Arrows indicate the direction of flow.

the colder tube. The cold stream of water will warm, the hot stream will cool; so at their point of departure, both streams of water approach the average of their two initial temperatures (figure 4.43a). If we take the same tubes and same starting temperatures but run the currents in opposite directions, we have a countercurrent exchange; heat transfer becomes much more efficient than if both currents flowed in the same direction (figure 4.43b). A countercurrent flow keeps a differential between the two passing streams throughout their entire course, not just at the initial point of contact. The result is a much more complete transfer of heat from the hot stream to the cold stream. When the tubes are separated, the cold stream is nearly as warm as the adjacent hot stream. Conversely, the hot stream gives up most of its heat in this countercurrent exchange, so that its temperature has fallen to almost that of the entering cold stream.

This physical principle of countercurrent exchange can be incorporated into the design of many living organisms. For example, endothermic birds that wade in cold water could lose much of their critical body heat to the icy water if warm blood circulated through their feet was exposed to the cold water. Replacing this lost heat could be expensive. A countercurrent heat exchange between outgoing warm blood in the arteries supplying the feet and returning cold blood in the veins prevents heat loss in wading birds. In the upper legs of such birds, small arteries come in contact with small veins, forming a **rete,** a network of intertwining vessels. Because arterial blood in these vessels passes in opposite directions to venous blood, a countercurrent system of heat exchange is established. By the time the blood in the arteries reaches the feet, it has given up almost all of its heat to the blood in the veins returning to the body. Thus, there is little heat lost through the foot into the cold water. The countercurrent system of the rete forms a **heat block,** preventing the loss of body heat to the surroundings. Estimates indicate that the rete is so efficient in heat transfer that if boiling water were poured through a wading bird's arteries at one end and ice water through its veins at the other end, blood vessels in the feet would lose less than 1/10,000 of a degree in temperature.

Respiration in many fishes is characterized by a countercurrent exchange also. Water high in oxygen flows across the gills, which contain blood capillaries low in oxygen flowing in the opposite direction. Because water and blood pass in opposite directions, gas exchange between the two fluids is very efficient.

In bird lungs, and perhaps in other animals as well, gas exchange is based on another type of flow, a stepwise crosscurrent exchange between blood and air capillaries. Because blood capillaries cross at nearly right angles to the air capillaries in which gas exchange occurs, a crosscurrent is created (figure 4.43c). Blood capillaries run sequentially from an arteriole to supply each air capillary. When blood capillaries cross an air capillary, oxygen passes into the bloodstream and CO_2 is given up to the air. Each blood capillary contributes stepwise to the rising level of oxygen in the venule it joins. Partial pressures vary along the length of an air capillary, but the additive effect of these blood capillaries in series is to build up efficient levels of oxygen in venous blood as it leaves the lungs.

Optics

Light carries information about the environment. Color, brightness, and direction all arrive coded in light. Decoding this information is the business of light-sensitive organs. However, the ability to take advantage of this information is affected by whether the animal sees in water or in air, and it is affected by how much the two eyes share overlapping fields of view.

Depth Perception

The position of the eyes on the head represents a trade-off between panoramic vision and depth perception. If the eyes are positioned laterally, each scans separate halves of the surrounding world, and the total field of view at any moment is extensive. Where visual fields do not overlap, an animal has **monocular vision.** It is common in animals preyed upon and gives the individual a large visual sweep of its environment to detect the approach of potential threats from most surrounding directions. Strict monocular vision, in which the visual fields of the two eyes are totally separate, is relatively rare. Hagfish, lampreys, some sharks, salamanders, penguins, and whales have strict monocular vision.

Where visual fields overlap, vision is **binocular vision.** Extensive overlap of visual fields characterizes humans. We have as much as 140° of binocular vision, with 30° of monocular vision on a side. Binocular vision is important in birds (up to 70°), reptiles (up to 45°), and some fishes (as much as 40°). Within the area of overlap, the two visual fields merge into a single **stereoscopic image** (figure 4.44). The advantage of stereoscopic vision is that it gives a sense of depth perception. Closing one eye and maneuvering about a room demonstrates how much sense of depth is lost when the visual field of only one eye is used.

Depth perception results from how the brain processes visual information. With binocular vision, the visual field seen by each eye is divided in the brain. In most mammals, half goes to the same side, and the other half crosses via the **optic chiasma** to the opposite side of the brain. For a given part of the visual field, inputs from both eyes are brought together on the same side of the brain. Within the brain, the **parallax** of the two images is compared. Parallax is the slightly different views one gets of a distant object when it is viewed from two different points. Look at a distant lamppost from one position, and then step a few feet laterally and look at it again from this new position.

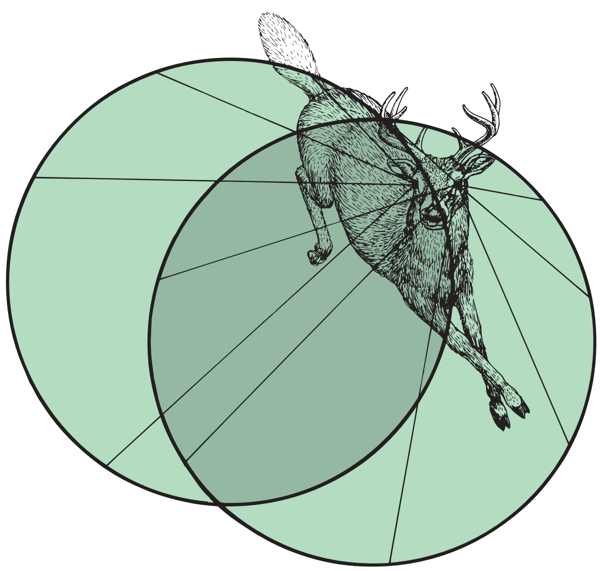


FIGURE 4.44 **Stereoscopic vision.** Where the conical visual fields of the deer overlap, they produce stereoscopic vision (shaded area).

Slightly more of one side of the lamppost can be seen, less of the opposite side, and the position of the post relative to background reference points changes as well. The nervous system takes advantage of parallax resulting from eye position. Each visual image gathered by each eye is slightly offset from the other because of the distance between the eyes. Although this distance is slight, it is enough for the nervous system to produce a sense of depth resulting from the differences in parallax.

Depth perception and stereoscopic vision (p. 688)

Accommodation

Sharp focusing of a visual image upon the retina is termed **accommodation** (figure 4.45a). Light rays from a distant object strike the eye at a slightly different angle than rays from a nearby object. As a vertebrate alters its gaze from close to distant objects of interest, the eye must adjust, or accommodate, to keep the image focused. If the image falls behind the retina, **hyperopia,** or farsightedness, results. An image focused in front of the retina produces **myopia,** or nearsightedness (figure 4.45b, c).

The lens and the cornea are especially important in focusing entering light. Their job is considerably affected by the **refractive index** of the media through which light passes, a measure of the bending effects on light passing from one medium to another. The refractive index of water is similar to the refractive index of the cornea; therefore, when light passes through water to the cornea in aquatic vertebrates, there is little change in the amount it bends as it converges on the retina. But when light passes through air to the liquid medium of the cornea in terrestrial vertebrates, it bends considerably. Similarly, aquatic animals viewing an object in air must compensate for the distortion produced by differences in the refractive indexes of air and water (figure 4.46). As a consequence of these basic optical differences, eyes are designed to work either in water or in air. Underwater vision is not necessarily out of focus. It just looks that way to our air-adapted eyes when we jump into a clear stream and attempt to focus our eyes. If we place a pocket of air in front of our eyes (e.g., a diving face mask), the refractive index our eyes are designed to accommodate returns and things become clear.

Accommodation can be accomplished by mechanisms that change the lens or the cornea. Hagfish and lampreys have a corneal muscle that changes the shape of the cornea to focus entering light. In elasmobranchs, a special protractor muscle changes the position of the lens within the eye. The elasmobranch eye is focused for distant vision. For near objects, the protractor muscle moves the lens forward. In most amniotes, the curvature of the lens changes to accommodate the eye's focus on objects near or far. Ciliary muscles act on the lens to change its shape and thus alter its ability to focus passing light (which, by the way, have nothing to do with microscopic cilia).

Eyes and mechanisms of accommodation (chapter 17)

Overview

Size matters; so does shape. Like any other characteristic of an organism, size and shape have survival consequences. Large organisms have fewer serious enemies. Small organisms find strength in numbers. But size and shape have physical consequences, in and of themselves. For a small

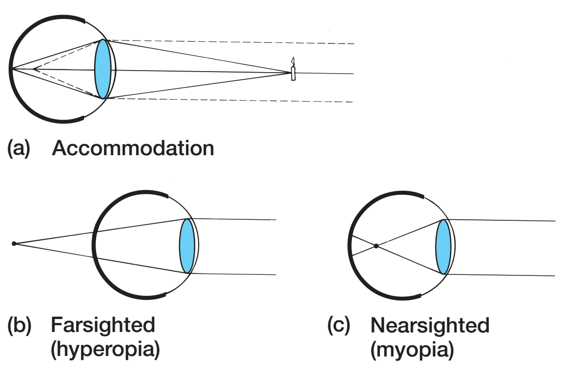


FIGURE 4.45 Accommodation. (a) Normal vision in which the image, solid lines, is in sharp focus on the retina of the eye. (b) Farsighted condition (hyperopia) in which the lens brings the light rays to focus behind the retina. (c) Nearsighted condition (myopia) in which the sharpest focus falls in front of the retina.

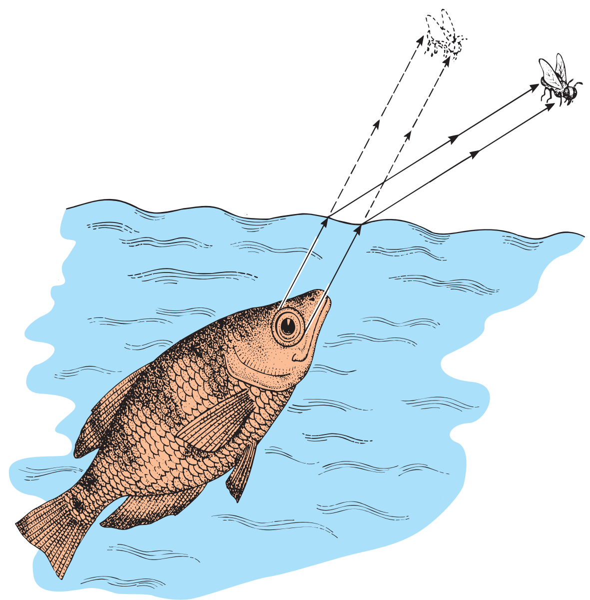


FIGURE 4.46 Refraction. Differences in the refractive indexes of water and air bend light rays that enter the water from the insect. The result makes the insect seem to be in a different position than it really is, indicated by the dashed lines. The archer fish must compensate in order to shoot a squirt of water accurately and hit the real, not the imaginary, image.

animal, gravity presents almost no dangers. Small lizards might scamper up walls and across ceilings. But for large animals, gravity may be more of a threat than predators. As J. B. S. Haldane reminds us, because of differences in scaling, a change in size inevitably requires a change in form. This is not for reasons of biology, but is instead a necessary consequence of geometry. Surface area increases rapidly with increase in size, scaling in proportion to the square of the linear dimensions; volume (mass) is even more affected, increasing by the cube of linear dimensions. Inevitably, larger organisms have relatively greater mass with which to contend and, consequently, the supportive and locomotor systems must be built differently and stronger to meet the accompanying physical demands.

Shape changes in proportion to size, termed *allometry,* are common during the growth of a young organism into the larger adult. These can be illustrated with graphs or transformation grids. The result, relative to body size, is often to accelerate the development of a body part, bring it to full size later in life when the adult is large enough and mature enough to use it. Shape is important for animals that move at significant speeds through fluids. A thin shape, presented to the fluid flow, helps reduce drag that would otherwise retard progress. Turned broadside, a fin or flipper uses profile drag to generate forces. A favorable shape, such as streamlining, encourages smooth, nonseparating flow. The Reynolds number tells us how changes in size and shape might affect performance of an animal in fluid, and emphasizes the importance of both in meeting physical demands of the fluid environment.

Forces, produced by muscles, are conveyed through levers, the skeletal system. The Newtonian laws of motion identify the physical forces an animal meets arising from inertia, motion, and action/reaction. When initiating motion, the bone-muscle system overcomes inertia, accelerates limbs or body into motion, and the contacted fluid or ground returns reaction forces. Muscles put a force into a lever system, and the lever system outputs that force as part of a task. The output to input ratio represents the mechanical advantage, a way of expressing whether a muscle has a leverage that increases either force output or speed output. Linked chains of jointed bones work as machines to transfer input forces from one part of the mechanism to another.

When conveying or receiving forces, the bone-muscle system itself is exposed to stresses that may be experienced as compression, tension, or shear forces. Failure level under each is different, with bones generally strongest in compression and most susceptible to breakage in shear. Further, the resulting stresses are carried unevenly within the skeletal element. Wolff's Law notices that bone remodels internally in proportion to the level and distribution of these stresses.

We also meet the fundamentals for gas diffusion and optics, which we will apply more fully in several of the later chapters.

In this chapter, we recognize that organisms face physical demands that endanger their survival. Consequently, we turn to the discipline that studies such a physical relationship between design and demands, namely, engineering. From this, we usefully apply its insights from biomechanics and biophysics to understand more of the adaptive basis of animal architecture.

Web Link

Visit the text website at *www.mhhe.com/kardong7e* for additional study aids including selected references, functional laboratories, and web links to chapter topics.