

Biomechanical Studies of Food and Diet Selection

Anthony Herrel, *UMR CNRS/MNHN, Department EGB, 55 rue Buffon, Paris, France*

Sam Van Wassenbergh, *Department of Biology, University of Antwerp, Belgium*

Peter Aerts, *Department of Biology, University of Antwerp, Belgium*

Based in part on the previous version of this eLS article 'Biomechanical Studies of Food and Diet Selection' (2004) by Anthony Herrel and Peter Aerts.

The ways animals acquire food are largely determined by the medium in which they feed. As water is dense and viscous, resistive forces are important and affect the way prey can be captured resulting in the independent evolution of suction feeding in many vertebrate groups. Alternatively, on land, gravitational forces play an important role and will affect prey capture and transport by imposing limits on the use of adhesive forces and thus tongue-based capture and transport. Biomechanical approaches involving the analysis of movements and forces can, combined with theoretical models, help explain the selective pressures operating on the feeding system. As such, these approaches may help explain the divergence of the feeding system in animals occupying different ecological niches and may help us understand the proximate factors driving adaptive radiations.

Introduction: Mechanics of Movement in Water Versus on Land

Whether an organism is moving in water or on land has major consequences for the biomechanics of movement. The physical properties of the two media are very different. Not only is water approximately 900 times denser than air, but also roughly 80 times more viscous. The consequences of these physical differences are numerous. One of the most notable effects is that the effect of gravitational forces acting on objects in water is small as they are counteracted by the hydrostatic lift, whereas the opposite is true in air. On the other hand, on land the resistance from the air on a moving body can usually be neglected as it is small. In water, however, the interaction between objects and the

eLS subject area: Ecology

How to cite:

Herrel, Anthony; Van Wassenbergh, Sam; and Aerts, Peter (June 2012) Biomechanical Studies of Food and Diet Selection. In: eLS. John Wiley & Sons, Ltd: Chichester.
DOI: 10.1002/9780470015902.a0003213.pub2

Advanced article

Article Contents

- Introduction: Mechanics of Movement in Water Versus on Land
- Prey Capture and Transport in Water
- Prey Capture and Transport on Land
- Mechanics of Mandibles and Jaws

Online posting date: 15th June 2012

moving fluid can be considerable and largely determine the dynamics of movement. Moreover, as aquatic feeding movements and biological movements in general are often highly unsteady and unpredictable, inertial effects, not only of the moving parts but also of the induced flow, must be considered (Aerts, 1990). (Note: in this article, we discuss biomechanical approaches to food and diet selection using mostly examples for vertebrates.)

Prey Capture and Transport in Water

Suction versus ram feeding: creating and controlling water currents

Water, being a very dense and viscous medium, poses very specific problems to predators wanting to capture prey in the water column. Because of these properties, predators moving towards prey will tend to generate a bow wave in front of the head that can potentially push the prey away from the predator (Lauder, 1985; Van Wassenbergh *et al.*, 2010). However, the properties of the medium can also be exploited by a predator to capture prey. Because of the law of continuity, any expansion of the buccal cavity will generate a flow of water from the external environment into the mouth. Prey items situated in the flow field will experience hydrodynamic forces (including the effect of the so-called added mass) and if these forces are large enough to overcome the inertia of the prey and/or to overcome the active or passive resistive forces of the prey (e.g. escape responses, adhering forces), the prey item will be carried by the flow into the mouth of the predator.

Water flow patterns resulting from buccal expansion vary in time and space (e.g. Day *et al.*, 2007): (1) at any position in the flow field, buccal expansion will cause the local flow velocity in the direction of the suction source to increase over time; (2) at any instant of the expansion, flow velocities typically show a decrease with the distance from the mouth as a result of the flow towards the mouth from all directions in three-dimensional space (Muller *et al.*, 1982). These changes in flow velocity (i.e. both temporal and spatial velocity gradients) go along with a spatial gradient of pressure in the water (due to the relationship described

by the Navier–Stokes equations) pressure is lowest inside the expanding buccal cavity and becomes gradually higher with increasing distance away from the mouth. For any prey item within this time-varying flow field, such a pressure gradient will result in a net pressure force on its surface in the direction of the predator's mouth. Previous studies showed that this pressure gradient is the dominant force for carrying relatively small, neutrally buoyant prey towards the predator, and that frictional forces (due to the velocity differences between prey and the surrounding water) only become important for relatively large, heavy, or escaping prey (Wainwright and Day, 2007; Van Wassenbergh and Aerts, 2009). To capture more 'resistive' prey, faster and larger expansions of the buccal cavity or, when the prey size allows this, a reduction of the mouth aperture are often desired since this will result in higher flow velocities and steeper pressure gradients. On the other hand, large negative pressures being generated within the buccal cavity require considerable muscular effort (Lauder, 1985; Carroll and Wainwright, 2006). This process of generating water flow to capture prey is typically called suction feeding.

For most aquatic vertebrates the suction process can be subdivided into two components, compensatory and inertial (Van Damme and Aerts, 1997). The first component involves an expansion that only compensates for the forward movement of the predator. Thus, no or little momentum is given to the water in front of the mouth (which would otherwise have pushed the prey aside). During compensatory suction there is essentially no predator-induced flow in the external frame of reference, and as a result prey displacements in this external frame of reference are absent (i.e. the prey does not move relative to its environment; note that it does move relative to the predator). Inertial suction consists of the generation of a backwards flow which draws the prey towards the predator or even through the entire buccal cavity. Here movements of the prey towards the predator can be observed in the external frame of reference. Thus, the prey is actively displaced towards the predator during inertial suction feeding. By expanding the buccal cavity in a rostral-caudal wave (the so called rostral-caudal or front-to-back expansion sequence) a continuous backwards flow is ensured (Lauder, 1985).

Both suction components can be combined to a varying extent, often dictated by the prey type. As neutrally buoyant food items behave like an element of water, they can easily be overtaken by compensatory suction alone. Elusive prey or heavy items to be sucked from the bottom, on the other hand, must be subjected to considerable hydrodynamic forces and inertial suction will be needed to draw the prey into the mouth. Inertial suction also requires less aiming accuracy from the predator, since the ingested parcel of water is less narrow and elongated as in compensatory suction (Higham *et al.*, 2006). Whereas most aquatic vertebrates are limited to the type of suction feeding described above, some fish use an alternative strategy: ram feeding. By swimming forward with both the mouth

and the opercular (and gill) slits wide open, fishes create a water flow through the mouth that exits the oral cavity through the gill slits (Lauder, 1985). In this way, fish can swim towards prey without needing the rapid, powerful expansion movements typical for suction feeding.

The rostral-caudal expansion wave used for prey capture often suffices to transport the food items directly towards the oesophagus or to the pharyngeal jaws. In other cases, for instance when large prey items are first held by the oral jaws, a so-called hydrodynamic tongue is used to transport food backwards. Basically, a series of rostral-caudal expansion waves similar to the ones used during prey capture will be used to generate a backwards flow carrying the prey step by step towards the oesophagus (Lauder, 1985).

Particle feeding, filters and mucous traps

Whereas active predation in water is widespread in vertebrates, most invertebrates employ a totally different strategy: particle, or suspension feeding (Rubenstein and Koehl, 1977). Because of their small size, most invertebrates have to feed at extremely low Reynolds numbers, which implies that viscous forces dominate their behaviour. This makes active predation much more difficult because they experience the water as a very viscous medium. However, not only invertebrates, but also the adult and larval stages of several vertebrate groups engage in filter feeding (tadpoles, fish, birds, whales). Particle feeding is based on the generation of a steady flow of water across a filter or sieve, which extracts particles from the surrounding water (Jørgensen, 1966; Lauder, 1985; **Figure 1**). In some filter feeding fishes it has been shown that the inhaled water enters parallel to the filtering surface (the gill sieve), whereas only clear filtrate exits through the gill sieve pores (Sanderson *et al.*, 2001). This mechanism is referred to as crossflow filtration, and avoids clogging of the filter.

The water flow can be generated by a variety of methods; it can be an existing water current, or alternatively it can be generated through movement of the organism. In most vertebrates that engage in suspension feeding the water stream is generated by modifications of the respiratory pump, or by swimming through the water with the mouth and gill cavity open resulting in continuous flow across the gills (essentially ram feeding; see above). Often, rhythmic expansions and contractions of the buccal cavity are used to pump water across the filter surfaces where particles can be retained. In many invertebrates, cilia or flagella are used to generate water currents. Invertebrates such as annelid worms that live in burrows will sometimes create external mucous traps in the tunnel, and generate water flow through undulatory body movements. Once enough particles have been retained in the trap, the mucus with adhering particles is eaten (Jørgensen, 1966).

In most filter-feeding systems, particles are filtered out by size, shape and density rather than food value. The rate of food accumulation is thus dependant on the water flow, which can be altered to fulfil the need of the organism. After

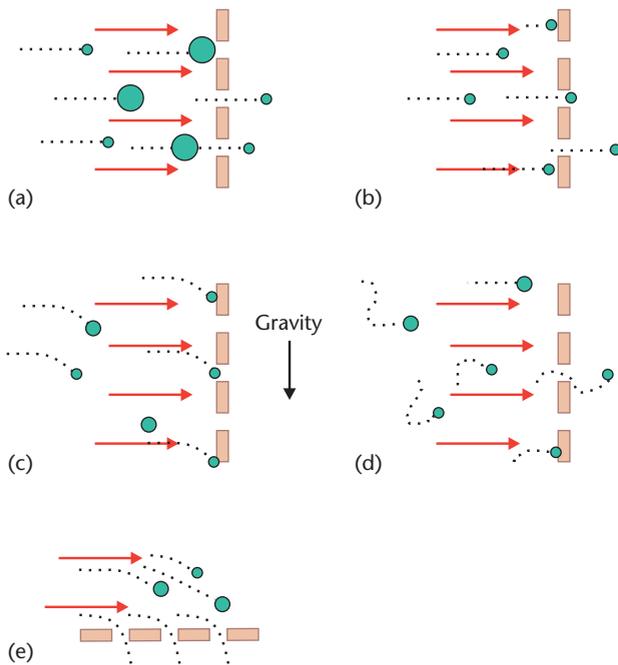


Figure 1 Suspension-feeding mechanisms have been classified into seven major groups: sieving, direct interception, inertial impaction, gravitational deposition, motile particle deposition, electrostatic attraction, and crossflow filtration. Sieving (a) is the simplest method and consists of retaining only those particles larger than the pores of the sieve. Direct interception and inertial impaction (b) are rather similar and rely on the retention of food particles on the mesh of the filter itself. In gravitational deposition (c), the particles are deposited on the filter through gravitational processes. Motile particle deposition (d), on the other hand, relies on the active movements of the particles independent of the water current to intersect with the filter. Electrostatic attraction is a filtering method that has been proposed for invertebrates and possibly also in anuran larvae. Here small particles are thought to adhere to the mucous layer covering filters due to electrostatic attraction forces. In crossflow filtration (e), the incoming flow is parallel with the filtering surface. This only allows passing of clear filtrate, whereas a gradually more condense particle-laden flow continues towards the oesophagus. (Modified after Rubenstein and Koehl, 1977; Lauder, 1985).

capture, however, particles may be sorted and only those of interest retained. The filter itself is often covered with mucus, and can be modified to trap certain types of particles by modifying the pore size of the filter (which can be achieved by muscular contraction). Also the rate of filter cleaning (as more food accumulates on the filter, the size of the particles sifted from the water column will change) and the diameter of the fibres in the mesh can have an effect on the types of particles retained (Jørgensen, 1966).

Prey Capture and Transport on Land

Because of the lower density and viscosity of air, suction feeding cannot be used to transfer food items to the mouth in a terrestrial environment. However, movements of predators towards prey can occur unhindered, making the prehension of prey by external structures the predominant

capture mode for terrestrial organisms. Prey-transport on the other hand becomes problematic on land (hydrodynamic transport does not function in air) and most terrestrial vertebrates have evolved a novel prey-transport organ: the tongue. In some groups such as frogs, salamanders, primitive lizards, some birds and mammals, the presence of a mobile tongue has been exploited to serve the function of prey capture as well. In most terrestrial vertebrates other structures such as beaks (e.g. birds, turtles), claws (carnivores, bats) or jaws (crocodiles, most birds, lizards, snakes and caecilians) are used to subdue prey and transfer it to the mouth. **See also:** [Ingestion in Reptiles and Amphibians](#)

As mentioned above, the tongue is used in most vertebrates to transport prey through the oral cavity. The mechanics of adhesion in tongues is based on adhesive bonding (typically wet adhesion where a thin layer of fluid is present between the tongue and prey), interlocking (the physical interaction of tongue surface irregularities with those on the prey surface) and occasionally suction (generation of negative pressure). Whereas adhesion and interlocking are common, suction forces probably play an important role only in chameleon tongues. As the forces generated through interlocking and wet adhesion are surface dependant (Emerson and Diehl, 1980), the transport of large prey will become problematic (for geometrically similar organisms surface area is proportional to mass $2/3$, implying that the mass of the food item increases at a faster rate than its surface area and yet it is the latter which determines the magnitude of the adhesive forces). Animals such as crocodiles, snakes, some lizards and birds that are known to transport large prey rely upon another mechanism: inertial transport (Gans, 1969). Inertial transport can be subdivided into two major types, static and kinetic. Whereas kinetic inertial transport relies on the inertia given to the prey by rapid head and neck movements of the predator to displace the prey posteriorly, static inertial transport relies on the inertia of the prey which allows the predator to move his head and body over the prey (Gans, 1969). These types of transport are most clearly exemplified by a bird transporting a large fish (kinetic inertial) or a snake eating a large mammal (static inertial). In the latter case the snake will literally crawl over the prey, using the inertia (i.e. mass) of the prey to pull its own body over it.

Mechanics of Mandibles and Jaws

Mandibles and jaws are external structures important in mechanical food reduction and the grasping of prey (see above). Organisms that do not possess structures allowing them physically to reduce the size of the prey are typically referred to as gape-limited predators. At least in vertebrates which cannot reduce prey, the maximal size of the prey that can be eaten is strictly limited by how wide these animals can open their jaws to allow the food to pass on to the oesophagus and digestive tract. Typical examples are most amphibians, nearly all species of snakes and many

birds. Once forceful jaws or mandibles evolve, predatory organisms can exploit new food items that would have been either too large to swallow, or impossible to digest (i.e. protected by an external cover that cannot be reduced chemically). The stronger the jaws or mandibles, the less time needed to reduce prey, making hard or large prey also energetically more interesting (i.e. less energy and time is spent processing the food).

Whereas increasing the force of jaws or mandibles thus seems an attractive evolutionary strategy, there is also a cost associated to being strong: the loss of speed. The evolutionary design of functional systems such as jaws or mandibles (including their associated musculature) is often governed by trade-offs between speed and force production. Trade-offs are caused by the different design constraints on systems built for speed versus force (Figure 2). At the muscular level, longer, parallel-fibred muscles (sarcomeres

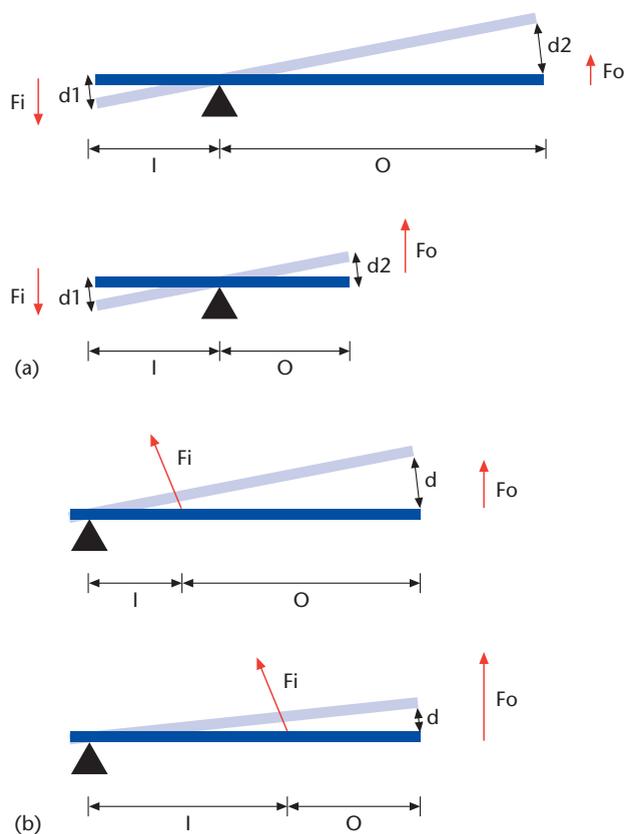


Figure 2 Biomechanical trade-offs between speed and force generation. (a) In simple lever systems the force exerted is determined by the input force (F_i) and the distance between the point of exertion of the input (I =inlever) and output forces (O =outlever, F_o =output force) and the fulcrum. The shorter O becomes, the larger the output force of the system (bottom panel). However, for a given force F_i the displacement (d_1 , d_2) within a given time increment will also be set by the length of the lever arms. If the length of the outlever O increases, the displacement d_2 in the same time period will be larger and thus the velocity of movement will be higher as well. (b) In a third order lever system, as is observed in the jaw closing system of mammals, the same rules apply. In a real jaw system, long jaws will result in a rapid closing and opening action and short jaws will be associated with a powerful bite.

in series) are typically faster, but to increase force, the cross-sectional area of the muscle must increase, and pennate muscles with the muscle fibres typically attaching at an angle to a central tendon are better (more sarcomeres in parallel; see Paul and Gronenberg, 1999). The biomechanics of fast versus forceful systems are also quite different. As jaws and mandibles essentially function as lever systems, speed will be enhanced by having a long outlever for a given inlever. Force production on the other hand will be optimised through a relatively short outlever. However, due to the direct relationship between force and acceleration it is not always possible to predict the speed of a given movement solely based on leverage characteristics (McHenry, 2011). Nevertheless, these biomechanical design principles have been used very successfully in the past to explain variation in crab claws, ant mandibles, and fish jaws, and to couple that variation to differences in the feeding ecology of these animals (e.g. Paul and Gronenberg, 1999). **See also: Vertebrate Functional Morphology and Physiology**

Among the extant vertebrates, mammals stand out because of their specialisation towards extensive food reduction before swallowing (Herring *et al.*, 2001). In primitive vertebrates such as most amphibians and reptiles, jaws are closed in the vertical plane and exert mostly simple shearing movements. Two exceptions to these simple systems are observed in the tuatara and in turtles. Both these groups of animals are capable of executing fore–aft translations of the jaws while closed. These movements allow them effectively to shear through tough materials such as skin or plant materials. Mammals, however, are the only extant vertebrates that have developed true grinding jaws as exemplified by the ungulates and rodents. These groups of animals show distinct modifications in the joint structure and jaw muscles that allow them to execute considerable movements in the horizontal plane. Jaw movements are characterised by a so-called power stroke after jaw closing (Herring *et al.*, 2001). The direction of this power stroke differs in rodents where the movement is from front to back, and ungulates where the movements are medio-lateral. These differences in movement patterns are coupled to a differential development of some of the jaw-closing muscles (e.g. the pterygoid muscle in ungulates and the masseter complex in rodents). Because of their ability to exert these grinding movements, mammals are the only extant vertebrates to have successfully and extensively radiated into the herbivorous niche (King, 1996). As plant cells are surrounded by a cell wall consisting of cellulose which cannot be digested by vertebrates, mechanical reduction of these cell walls is a prerequisite for herbivory. **See also: Ingestion in Mammals**

Because biomechanical analyses have been so successful in explaining patterns of variation in the feeding system of extant vertebrates (Figure 3), they have often been used to infer feeding habits and lifestyle of extinct vertebrates (Norman and Weishampel, 1991). Using biomechanical approaches such as static jaw modelling and modern engineering techniques such as finite element analysis (see

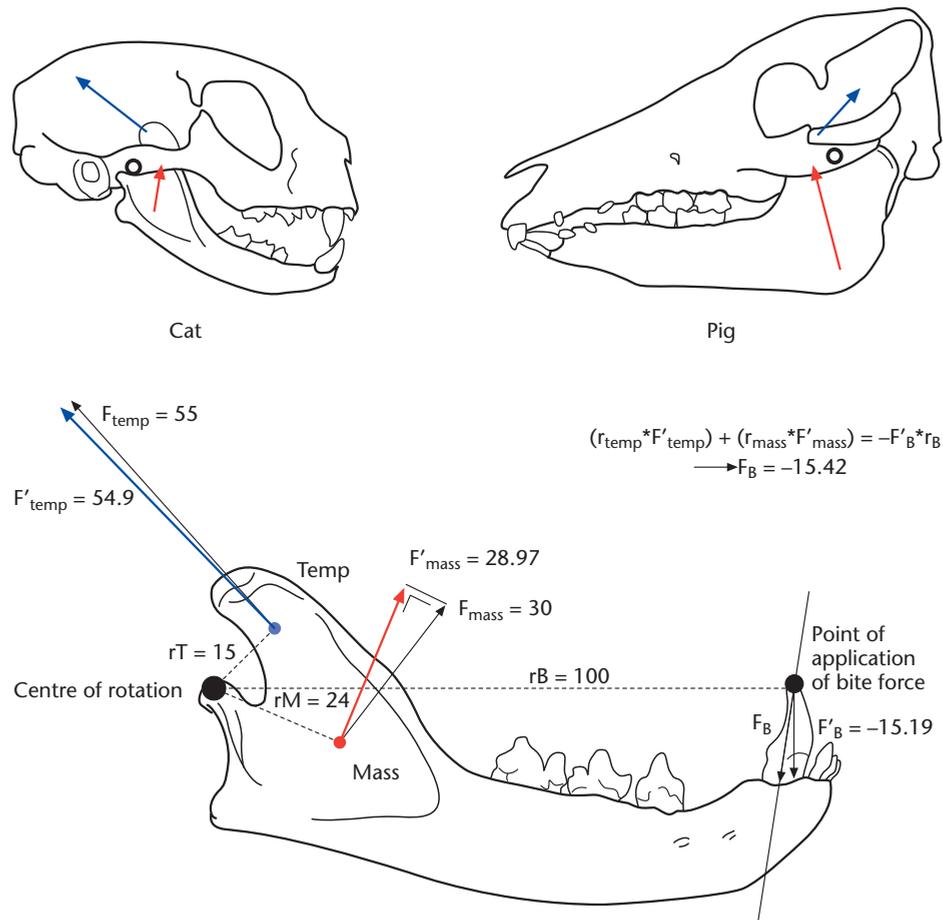


Figure 3 Biomechanical analysis of mammalian skulls. Depicted are schematic representations of the skull of a carnivore (cat) and an omnivore (pig). Note how the fulcrum is positioned much higher up the jaw in the case of the pig. This allows omnivores and herbivores to exert grinding movements (entire tooth row in contact upon closure). In carnivores, on the other hand, the jaws exert a cutting motion. Also indicated are the force vectors exerted by the jaw muscles. The temporalis (blue), and the masseter (red) muscle vectors are shown. The size of the arrow indicates the importance of the muscle. Whereas in carnivores the temporalis is the largest jaw-closer muscle, in omnivores and herbivores the masseter is the largest jaw-closer muscle. Note also how the position of the biggest muscle groups is such that in carnivores maximal force is generated with open jaws, and in omnivores and herbivores with closed jaws (i.e. the line of action of the muscle is optimal). r_B , moment arm bite force; r_T , moment arm temporalis muscle; r_M , moment arm masseter muscle; F_B , bite force.

below), both palaeontologists and neontologists alike are beginning to understand the enormous diversity in skull form among vertebrates (Rayfield, 2007). Biomechanical estimates of skull strength, bite force, and jaw movement patterns have been used to infer feeding style and activity patterns of dinosaurs. These analyses show that dinosaurs differ from present-day reptiles in the diversity of form and use of the cranial system. More like modern mammals, dinosaurs show a variety of cranial specialisations that allowed them to exploit very successfully a variety of feeding niches, including herbivory. Among both ornithischians and saurischians novel grinding systems evolved that presumably formed the basis of large and successful radiations of herbivorous forms. Also among the carnivorous saurischians a wide variety of skull forms are observed that are related to different lifestyles. Whereas some, such as *Tyrannosaurus rex*, were presumably active predators with a powerful bite, others, for example,

Allosaurus, most likely used rapid slashing bites that resulted in the prey bleeding to death. **See also:** [Biomechanics: Principles](#)

Teeth: the interaction of jaws and food

Being the interface between jaws and food, teeth play an important role in transferring forces which should ultimately result in the mechanical breakdown of the food. Food items are very heterogeneous materials which are not easily reduced. For many of them, initial crack formation and further crack propagation are extremely important (Vincent and Lillford, 1991). Based on their mechanical properties, food items can be classified as brittle (e.g. nuts, snails, biscuits, chocolate), ductile (e.g. cheese, earthworms, fruits), ductile–brittle (e.g. hard fruits such as peaches, apple) and fibrous (e.g. meat, skin, leaves). For each of these food categories certain tooth types will be

most efficient in causing food reduction (Sibbing, 1991). The size of the food–tooth contact area (which is dependent on food type for a given tooth shape) will determine the magnitude of the stresses in the food and thus its efficiency in reducing the food. Based on the shape and movement of the teeth they can be divided into distinct functional types (Figure 4). Crushing teeth will be most useful in reducing brittle foods. Splitting or piercing teeth will maximise stress on the food and will result in tooth penetration causing internal crack propagation. By adding movements other than simple dorsoventral ones, the effectiveness of the teeth can be greatly increased. Thus cutting, lacerating and grinding are more effective than crushing, splitting or piercing (Figure 4). Recently, new methods have been developed to quantify the complex shapes as observed in mammalian teeth (Evans *et al.*, 2007). These methods have successfully been applied to analyses of dental complexity in bats explaining the co-variation between tooth structure, bite force and diet (Santana *et al.*, 2011). **See also: Plant Biomechanics**

Bite forces: biomechanical estimates and *in vivo* measurements

The biomechanics of jaws and mandibles have been analysed in a variety of organisms. Often researchers have tried to estimate bite forces of animals. To do so, static biomechanical models have most often been employed. These models often rely on what is called a free body approach. In such an approach the segment of interest (e.g. the jaw of an animal) is considered as a free body (taken out of its context with the other bones in the skull) and the force and moment equations are solved with the premise that the system must remain static (i.e. this implies that the sum of all external forces or moments acting on the free body must be zero). By estimating the external forces acting on such a free body (e.g. the muscle forces which are usually based on morphological estimates of muscle size) the equilibrium equations can be solved and bite forces can be calculated. More complex approaches such as dynamic models where the forces are estimated throughout the movement are sometimes also used to gain insights into the function of the jaws (Curtis, 2011). More recently, the use of finite element analysis has become popular (Rayfield, 2007; Dumont *et al.*, 2009; Soons *et al.*, 2010). Although mathematically quite complex and requiring information on the three-dimensional structure and shape of the elements, this approach allows the accurate calculation of bite forces as well as the forces on any given element in the skull and can be coupled to three-dimensional quantifications of cranial shape (O'Higgins *et al.*, 2011). These modelling approaches have been used very successfully to estimate bite forces in a variety of reptiles and mammals (Figure 5).

Besides these more theoretical methods, a number of more experimental approaches have been used as well to gain insights into the forces produced by organisms. One of the methods often used is an indentation test. In these tests the animal is allowed to bite on a deformable material.

After being bitten, the depth of tooth penetration in the material can be measured and compared to experimental indentations (using known forces) created in the same material using the teeth of the animal (Erickson *et al.*, 1996). Other indirect approaches involve breaking tests. Here the animal is given different food items of known strength. The hardest food item that can still be crushed by the animal then corresponds to an estimate of the maximal bite force of that animal. Actual direct experimental estimates of bite force are becoming more and more common as well (Dean *et al.*, 1992; Herrel *et al.*, 1999, 2002; Erickson *et al.*, 2001; Anderson *et al.*, 2008). These direct measures usually involve the use of bite bars equipped with strain gauges registering the deformation of the bar when bitten by an animal (Binder and Van Valkenburg, 2000). By calibrating the bars using weights of known masses the forces can be calculated. Other methods involve the use of piezoelectric transducers built into a lever system. The animal bites on the lever, transmitting force to the transducer which deforms the crystal. As the piezoelectric crystal emits a current proportional to its deformation, the forces needed to deform the crystal can be measured. A comparison of maximal bite forces generated by a wide variety of animals plotted in Figure 5 shows that size plays an important role. Whereas the absolute bite forces of a *T. rex* are obviously large, they are rather small when scaled down to the size of some lizards.

Internal mechanical systems for processing food, gizzards

Although many animals reduce food items using external structures, some rely entirely on internal structures to reduce food. The simplest way of doing this is by ingestion of alien objects such as stones or dirt. In the stomach, these will act as grinding stones to reduce ingested food items. This strategy, called litho- or geophagy, is common among reptiles (King, 1996). Many lizards, dinosaurs and birds employ this strategy to help reduce otherwise tough food items such as plants. In birds, more specialised muscular compartments called gizzards are often present. Because these animals are constrained by flight (having teeth or heavy skulls would compromise their flight capacity) part of the stomach is modified to grind up food. As the stomach is situated at the level of the centre of mass, having a large muscular stomach does not disrupt the balance of the animals during flight. Often this strategy is combined with the ingestion of stones or dirt. As a consequence of the lack of external grinding structures, true leaf-eating herbivorous birds are generally rare (King, 1996).

More specialised internal systems, for example, pharyngeal jaws, are found in fish. These plate-like structures, consisting of modified pharyngeal elements, are situated at the back of the mouth and can be pushed against each other by specialised branchial muscles. Fish specialising on snails as food show strongly developed pharyngeal jaws and hypertrophied adductor muscles that allow them to crush molluscs before ingesting them. Extensive research into the

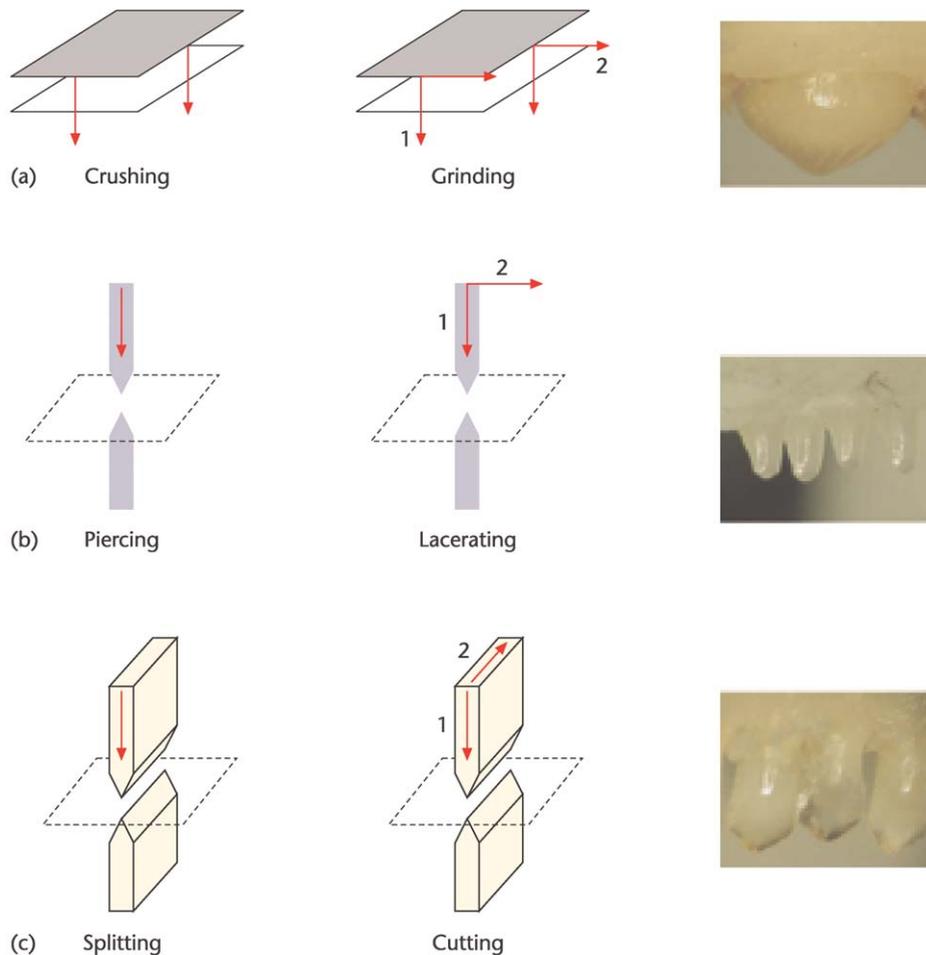


Figure 4 Tooth shape and function. (a) Where two flat surfaces are moved towards each other crushing is achieved. By adding a translation component to the movement, a grinding action is added to the system. Note that the addition of irregularities on the surface of the teeth will greatly improve the efficiency of the movement. The tooth of a blue-tongued skink (*Tiliqua scincoides*) is shown to illustrate a typical crushing tooth. This animal uses its teeth to crush hard objects such as snails. (b) If pointed teeth are brought together in a dorsoventral plane a piercing movement is the result. By adding a translational component, a lacerating action is created. As illustration, the teeth of a tokay gecko (*Gekko gekko*) are shown. These simple, pointed teeth are used to pierce the exoskeleton of small arthropods. (c) When the teeth become sharp ridges, splitting will be the result of movements in the dorsoventral plane. By adding movements parallel to the long axis of the ridge, a cutting action can be achieved. The teeth of a large herbivorous scincid lizard (*Corucia zebrata*) are shown as illustration of this tooth type. These teeth are used to crop small pieces from larger leaves. Modified after Sibbing (1991).

pharyngeal jaws of fish using biomechanical models has demonstrated that the pharyngeal jaws rapidly respond to changes in the mechanical properties of food items. In the cichlid fishes of the great African lakes it has been demonstrated that this ability to respond plastically to different food items has played an important role in their rapid evolutionary diversification and explosive radiation. A unique internal reduction system is observed in the case of egg-eating snakes. As mentioned earlier, snakes are gape-limited predators which typically do not reduce prey before ingestion. Egg-eating snakes, however, have developed a novel system to deal with large prey encased by an indigestible shell. In these animals, the hypophyses (ventral projections of the vertebrae) of the first seven cervical vertebrae have been enlarged. After the egg has been ingested, it is pushed by the throat constrictor muscles

against these enlarged projections to break the shell. The snake will then regurgitate the eggshell and ingest the highly nutritious egg content.

Mechanical defences against herbivory and predation

Naturally, organisms functioning as prey will respond to increased predation pressures, and this has resulted in elaborate mechanical and chemical defences against predation. Plants probably show the widest diversity of responses and have evolved an impressive array of chemical defences. However, mechanical defences against herbivory are also common and include the presence of spiny structures (needles, spines, thorns), the inclusion of silicates into cells which cause rapid abrasion of the teeth of

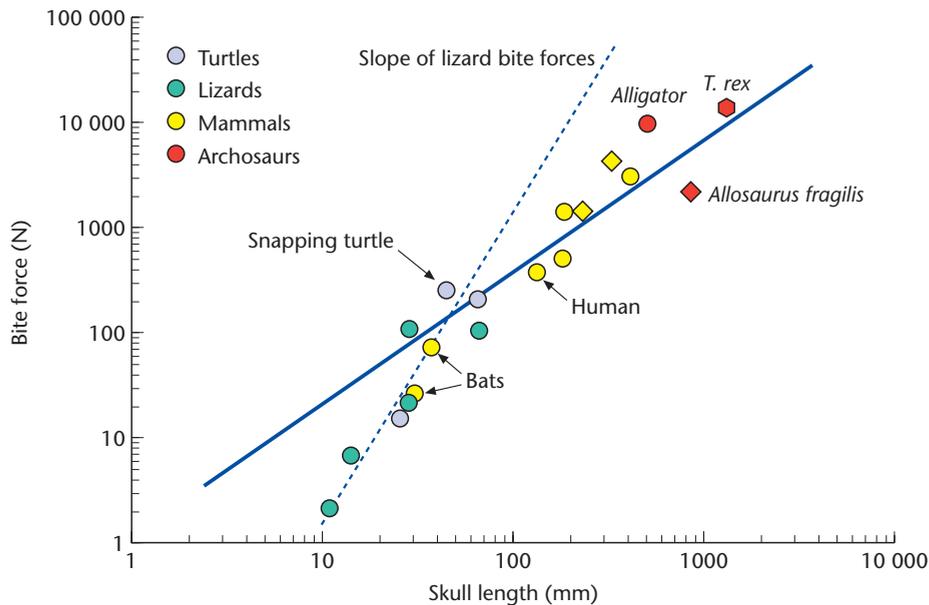


Figure 5 The effect of body size on bite forces in vertebrates. Depicted are the sizes of skulls and corresponding bite forces for different taxa. In black the theoretical scaling of length to force is indicated (slope=2), and the dashed line represents the scaling line for lizard and turtle bite forces. Note how in lizards and turtles bite force increases much faster with skull length than in mammals or archosaurs. This implies that if one scaled a lizard up to the size of a *Tyrannosaurus rex*, it would be biting at least ten times as hard. Data from *in vivo* studies are indicated with circles, from modelling studies with diamonds and from indentation studies with hexagons. (Based on data gathered by the authors for bats and turtles and lizards; Thomason, 1991; Dean *et al.*, 1992; Lindner *et al.*, 1995; Erickson *et al.*, 1996, 2001; Binder and Van Valkenburg, 2000; Rayfield *et al.*, 2001; McBrayer and White, 2002).

herbivores and the creation of fibrous materials which are extremely difficult to reduce. The co-evolution of predator and prey has led to large-scale evolutionary patterns. A nice example is the rise and diversification of sauropodomorphs coinciding with that of the gymnosperms in the Jurassic and the rise of the angiosperms in the Cretaceous followed by the diversification of the ornithopods and ceratopians (Norman and Weishampel, 1991).

Among animals both chemical defences and external mechanical defences are also common. Obvious examples are the exoskeletons of certain arthropods (e.g. beetles), the carapace of turtles, armadillos, glyptodonts and many extinct vertebrates. Other obvious defensive mechanisms are the spines and quills in hedgehogs and porcupines, or the horns in triceratops and stag beetles. Whenever specialisations of predators evolve, prey will show an evolutionary response to counter the novel predatory strategy. That strong selection on predatory strategies can lead to spectacular behavioural strategies as well as mechanical ones is nicely illustrated by the use of stones to crush hard-shelled clams in sea otters, or the use of tools by some Darwin finches to extract insect larva e from under bark.

References

- Aerts P (1990) Mathematical biomechanics and the 'what', 'how' and 'why' in functional morphology. *Netherlands Journal of Zoology* **40**: 153–172.
- Anderson R, McBrayer LD and Herrel A (2008) Bite force in vertebrates: opportunities and caveats for use of a nonpareil whole-animal performance measure. *Biological Journal of the Linnean Society* **93**: 709–720.
- Binder WJ and Van Valkenburg B (2000) Development of bite strength and feeding behaviour in juvenile spotted hyenas (*Crocuta crocuta*). *Journal of Zoology, London* **252**: 273–283.
- Carroll AM and Wainwright PC (2006) Muscle function and power output during suction feeding in largemouth bass, *Micropterus salmoides*. *Comparative Biochemistry and Physiology, Part A* **143**: 389–399.
- Curtis N (2011) Craniofacial biomechanics: an overview of recent multibody modelling studies. *Journal of Anatomy* **218**: 16–25.
- Day SW, Higham TE and Wainwright PC (2007) Time resolved measurements of the flow generated by suction feeding fish. *Experiments in Fluids* **43**: 713–724.
- Dean JS, Throckmorton GS, Eliis EE and Sinn DP (1992) A preliminary study of maximum voluntary bite force and jaw muscle efficiency in pre-orthognathic surgery patients. *Journal of Oral Maxillofacial Surgery* **50**: 1284–1288.
- Dumont ER, Grosse IR and Slater GJ (2009) Requirements for comparing the performance of finite element models of biological structures. *Journal of Theoretical Biology* **256**: 96–103.
- Emerson SB and Diehl D (1980) Toe pad morphology and mechanisms of sticking in frogs. *Biological Journal of the Linnean Society* **13**: 199–216.
- Erickson GM, Lappin AK and Vliet K (2001) Ontogeny of bite-force performance in the American alligator *Alligator mississippiensis*. *American Zoologist* **41**(6): 1437–1438.

- Erickson GM, Van Kirk SD, Su J *et al.* (1996) Bite force estimation for *Tyrannosaurus rex* from tooth marked bones. *Nature* **382**: 706–708.
- Evans AR, Wilson GP, Fortelius M and Jernvall J (2007) High-level similarity of dentitions in carnivorans and rodents. *Nature* **445**: 78–81.
- Gans C (1969) Comments on inertial feeding. *Copeia* **1969**(4): 855–857.
- Herrel A, O'Reilly JC and Richmond AM (2002) Evolution of bite performance in turtles. *Journal of Evolutionary Biology* **15**: 1083–1094.
- Herrel A, Spithoven L, Van Damme R and De Vree F (1999) Sexual dimorphism of head size in *Gallotia galloti*; testing the niche divergence hypothesis by functional analyses. *Functional Ecology* **13**: 289–297.
- Herring SW, Rafferty KL, Liu ZJ and Marshall CD (2001) Jaw muscles and the skull in mammals: the biomechanics of mastication. *Comparative Biochemistry and Physiology - Part A* **131**: 207–219.
- Higham TE, Day SW and Wainwright PC (2006) Multidimensional analysis of suction feeding performance in fishes: fluid speed, acceleration, strike accuracy and the ingested volume of water. *Journal of Experimental Biology* **209**: 2713–2725.
- Jørgensen CB (1966) *Biology of Suspension Feeding*. Oxford: Pergamon Press.
- King G (1996) *Reptiles and Herbivory*. London: Chapman and Hall.
- Lauder GV (1985) Aquatic feeding in lower vertebrates. In: Hildebrand M, Bramble DM, Liem KF and Wake DB (eds) *Functional Vertebrate Morphology*, pp. 210–229. Cambridge, MA: Harvard University Press.
- Lindner DL, Marretta SM, Pijanowski GJ, Johnson AL and Smith CW (1995) Measurement of bite force in dogs: a pilot study. *Journal of Veterinary Dentistry* **12**: 49–52.
- McBrayer LD and White TD (2002) Bite force, behavior, and electromyography in the teiid lizard *Tupinambis teguixin*. *Copeia* **2002**: 111–119.
- McHenry MJ (2011) There is no trade-off between force and velocity in a dynamic lever system. *Biology Letters* **7**: 384–386.
- Muller M, Osse JWM and Verhagen JHG (1982) A quantitative hydrodynamical model of suction feeding in fish. *Journal of Theoretical Biology* **95**: 49–79.
- Norman DB and Weishampel DB (1991) Feeding mechanisms in some small herbivorous dinosaurs: processes and patterns. In: Rayner JMV and Wootton RJ (eds) *Biomechanics in Evolution*, pp. 161–181. Cambridge: Cambridge University Press.
- O'Higgins P, Cobb S, Fitton LC *et al.* (2011) Combining geometric morphometrics and functional simulation: an emerging toolkit for virtual functional analyses. *Journal of Anatomy* **218**: 3–15.
- Paul J and Gronenberg W (1999) Optimizing force and velocity: muscle fibre attachments in ants. *Journal of Experimental Biology* **202**: 797–808.
- Rayfield EJ (2007) Finite element analysis and understanding the biomechanics and evolution of living and fossil organisms. *Annual Reviews of Earth and Planetary Sciences* **33**: 541–576.
- Rayfield EJ, Norman DB, Horner CC *et al.* (2001) Cranial design and function in a large theropod dinosaur. *Nature* **409**: 1033–1037.
- Rubenstein DI and Koehl MAR (1977) The mechanisms of filter feeding: some theoretical considerations. *American Naturalist* **111**: 981–994.
- Sanderson SL, Cheer AY, Goodrich JS, Graziano JD and Callan WT (2001) Crossflow filtration in suspension-feeding fishes. *Nature* **412**: 439–441.
- Santana SE, Strait S and Dumont ER (2011) The better to eat you with: functional correlates of tooth structure in bats. *Functional Ecology* **25**: 839–847.
- Sibbing FA (1991) Food processing by mastication in cyprinid fish. In: Vincent JFV and Lillford PJ (eds) *Feeding and the Texture of Food*, pp. 57–92. Cambridge: Cambridge University Press.
- Soons J, Herrel A, Genbrugge A *et al.* (2010) Mechanical stress, fracture risk, and beak evolution in Darwin's ground finches (*Geospiza*). *Philosophical Transactions B* **365**: 1093–1098.
- Thomason JJ (1991) Cranial strength in relation to estimated biting forces in some mammals. *Canadian Journal of Zoology* **69**: 2326–2333.
- Van Damme J and Aerts P (1997) Kinematics and functional morphology of aquatic feeding in Australian snake-necked turtles (Pleurodira; Chelodina). *Journal of Morphology* **233**: 113–125.
- Van Wassenbergh S and Aerts P (2009) Aquatic suction feeding dynamics: insights from computational modelling. *Journal of the Royal Society Interface* **6**: 149–158.
- Van Wassenbergh S, Brecko J, Aerts P *et al.* (2010) Hydrodynamic constraints on prey-capture performance in forward-striking snakes. *Journal of the Royal Society Interface* **7**: 773–785.
- Vincent JFV and Lillford PJ (1991) *Feeding and the Texture of Food*. Society for Experimental Biology seminar series 44. Cambridge: Cambridge University Press.
- Wainwright PC and Day SW (2007) The forces exerted by aquatic suction feeders on their prey. *Journal of the Royal Society Interface* **4**: 553–560.

Further Reading

- Bels VL, Chardon M and Vandewalle P (1994) *Advances in Comparative Environmental Physiology, vol. 18: Biomechanics of Feeding in Vertebrates*. Berlin: Springer Verlag.
- Bramble DM and Wake DB (1985) Feeding mechanisms of lower tetrapods. In: Hildebrand M, Bramble DM, Liem KF and Wake DB (eds) *Functional Vertebrate Morphology*, pp. 230–261. Cambridge, MA: Harvard University Press.
- Ferry-Graham LA and Lauder GV (2001) Aquatic prey capture in fishes: a century of progress and new directions. *Journal of Morphology* **248**: 99–119.
- Gans C (1974) *Biomechanics, an Approach to Vertebrate Biology*. Philadelphia: JB Lippincott.
- Hanken J and Hall BK (1993) *The Skull, Functional and Evolutionary Mechanisms*. Chicago: University of Chicago Press.
- Schwenk K (2000) *Feeding: Form, Function and Evolution in Tetrapod Vertebrates*. San Diego: Academic Press.
- Turnbull WD (1970) Mammalian masticatory apparatus. *Fieldiana Geology* **18**: 149–356.