DEMOGRAPHIC RESEARCH

Research Article

Trajectories and models of individual growth

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Abstract

It has long been recognized that the patterns of growth play an important role in the evolution of age trajectories of fertility and mortality (Williams, 1957). Life history studies would benefit from a better understanding of strategies and mechanisms of growth, but still no comparative research on individual growth strategies has been conducted.

Growth patterns and methods have been shaped by evolution and a great variety of them are observed. Two distinct patterns – determinate and indeterminate growth – are of a special interest for these studies since they present qualitatively different outcomes of evolution. We attempt to draw together studies covering growth in plant and animal species across a wide range of phyla focusing primarily on the noted qualitative features. We also review mathematical descriptions of growth, namely empirical growth curves and growth models, and discuss the directions of future research.

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1   Introduction

The ontogenetic growth of an individual is intuitively understood to be an increase in the size of the whole organism or parts of it with age. But the very "natural" notion of growth is, in fact, very difficult to define. Living organisms are complex systems, consisting of parts that often grow at different rates and displaying different patterns. Some parts of the body may grow faster than others, some may stop growing at a certain stage while others continue to grow, and organs may grow "on demand" during regeneration. The cells of an organ may divide continuously throughout an organism's life, replacing aging cells and producing cell turn-over in the tissues; still the body size may remain constant.

Growth is coordinated by a program of ontogenetic development that allows for variability in the development rates and sizes in order to adapt to environmental conditions. Size and growth rates are subject to evolutionary optimization and constraints. On the one hand, larger size usually leads to greater mating success, greater fertility, lower vulnerability to environmental hazards, and thus lower mortality. On the other, growth needs resources, and trades-off with other traits.

Studies on growth and maintenance shed light on the problem of senescence. Most organisms experience cell turn-over in most tissues. Some organisms (e.g. hydra) apparently escape senescence due to a quick turn-over of cells (Martínez, 1998).

Growth and body size are strongly related to other traits and fitness. Research on extant species showed a strong statistical relationship between body mass and a remarkable variety of biological features (Smith, 1996).

Measures of growth
Growth as an increment in size can be measured in many different ways, each having advantages and drawbacks. An increase in mass or volume often can be measured easily, but may be only indirectly related to growth as increase in biomass. Organisms may change in content of water or fat, in mass and volume, but this is not considered as growth. To account for such changes, measurements of dry and fat-free mass have been developed. However, these measurements are often destructive. Non-destructive methods of body composition measurement include X-ray absorptiometry, electrical impedance, and imaging techniques (see (Heymsfield et al., 2005) for a comprehensive review).

In some cases, it may be hard or impossible to measure mass, e.g. in rooted plants, embryos or tiny organisms, but linear measurements (such as of the wing span of birds, of the nose-tail of rodents, and of the length of small organisms such as flies) are easier to take; thus they are used as proxies to estimate mass. This method is complicated, however, because volume and mass estimation by linear size requires knowledge of body density and of the so-called "shape coefficient". Measuring growth as a dynamics of some linear body measure is widely used. These issues are discussed in detail in (Kooijman, 2000).

The growth of small multicellular organisms can be measured as an increase in the number of cells. In certain cases, the volume and mass of cells may change without a corresponding change in cell numbers (e.g. during muscle training).

It seems impossible to propose a single definition and measure of growth suitable to all applications. Different studies employ different measures of size and growth, such as mass and volume, and different linear measurements, such as dry, fat-free mass, bone-free mass, and cell counts. But the different measures are often incompatible with each other, and conversion between them often includes unknown factors, such as shape, body density, fat, bone or water contents. This is why caution should be taken when comparing growth measured in different ways (an example of such difference is illustrated in Figure 8).

Length, volume, and shape

The volume of an organism is related to its linear measures in different ways, depending on the construction of the organism. Several main types of constructions can be distinguished. In isomorphically growing organism, all linear dimensions change proportionally, and volume V is related to any of its linear measures, L as $V = \alpha L^3$, where α is a shape parameter. If the shape does not change, α=const. Typically, organisms change shape as they increase in size, so the value of shape parameter α changes. Some organisms, having the shape of sheets, films, and flat bodies with a constant, but small height (such as leaves), grow in two dimensions. In such organisms, $V = \alpha L^2$. Some organisms have the shape of sticks or rods and grow only in one dimension. The relation between the linear measure and volume in them is $V = \alpha L$. The volume is proportional to the surface area in the latter two types. A detailed description of the relations between volume and linear size be found in (Kooijman, 2000, chapter 2.2.2).

Methods of growth

Animals and plants are constituted of parts that, during ontogeny, may grow at different rates and according to different patterns. For example, tree branches and tree roots can grow indefinitely, whereas leaves and flowers show a clear determinate pattern. Several "ways" or methods of growth can be distinguished (after Raup and Stanley (1978)):

Accretion – adding new material to an existing skeleton. This kind of growth is typical for mollusks, trees (growth rings), fish scales, and the teeth of some vertebrates.

Adding new parts – in this way, trilobites add additional segments, echinoderms add new plates and cephalopods. Segmented organisms (such as bamboos) add new segments.

Molting – the periodic shedding of skin or of the external skeleton (exoskeleton) and the formation of new one after a burst of rapid growth. This is typical for arthropods. Trilobite molt and grow rapidly between instars (molts). The growth of snakes is also

accompanied by moulting. In such organisms, the skin or exoskeleton protects the organism, but also limits expansion; thus it is periodically replaced with a new, larger skin or exoskeleton.

Modification – the re-formation and re-shaping of the original material as size increases. Vertebrate bones grow in this fashion.

Often, a mixture of growth patterns is observed. Trilobites add segments while molting. Echinoderm plates accrete and new ones are also added; cephalopods both accrete and add walls between chambers.

Growth can be continuous or discontinuous. Examples of discontinuous growth are clams in the gulf of California. Their growth starts in late March, speeds up in spring and early summer, slows or stops, speeds up again, and then stops in late November. Discontinuous, pulsed growth can be observed in perennial organisms – they grow rapidly in the beginning of the season and decrease or shut down growth and other metabolic activities between the seasons to survive.

The so-called "catch-up" growth is observed in organisms with a genetically determined target size. When early life conditions (usually the lack of food) disfavor the growth of an individual in comparison to others, the latter may catch-up with their more "lucky" competitors later in life. Such growth pattern can be found in birds.

"Growth on demand" — the regeneration observed both in determinate and indeterminate growing organisms (e.g. wound closing; liver regeneration in humans; tail regeneration in reptiles; leg, eye, and tail regeneration in axolotl (Tanaka, 2003)) can also be observed.

Qualitative types of growth

Growth patterns are traditionally classed in two groups: determinate and indeterminate ones. They have two principally different features, presumably demonstrating different optima of life history evolution.

Determinate growth is usually defined as growth that stops when an organism reaches a certain size. Usually growth stops during the reproductive stage. Indeterminate growth is defined as growth that continues past maturation and may continue to the end of life (Heino and Kaitala, 1999).

Determinate growth is observed in bacteria and other unicellular organisms, all birds, some plants, fish, insects, and most mammals. They rapidly grow to a pre-defined adult size, at which physical growth stops, and then mature at a characteristic adult size. Some organisms (such as the Nematode worm, the fruit fly *D. melanogaster*, *C. capitata*) have a posmitotic adult stage (imago), at this stage cells do not divide and there is no growth.

Indeterminate growth is characteristic of a large number of invertebrate taxa – some kinds of algae, clams, cladocerans and crayfish, mollusks, many insects, echinoderms,

many modular animals such as corals and sponges, and "lower" vertebrate taxa, such as most fish, amphibians, and reptiles (lizards and snakes). It is also found in perennial plants and most trees (Lika and Kooijman, 2003; Vaupel et al., 2004). The best studied animals that exhibit indeterminate growth are sea urchins (*Strongylocentrotus*) and salmon. The adult size of these organisms depends largely on the environmental conditions they live in. In theory, they can get as large as their environment and diet allow.

The literature commonly notes that all mammals and even "all higher vertebrates" grow determinately. But male eastern and western grey kangaroos, wallabies, pademelons and swamp wallabies, American bisons, giraffes, African and Indian elephants, mule deer, and white-tailed deer seem to grow after maturity and throughout their life and hence to have have indeterminate growth. The females of these species can grow determinately. Thus indeterminate growth can also be enjoyed by higher organisms.

Both growth strategies can occur even among closely related taxa: cladocerans show indeterminate growth (*Daphnia magna* can grow by a factor of two in length, i.e. a factor eight in volume, during the reproductive period), while copepods show determinate growth (Kooijman, 2000, p. 293), both being members of the phylum *Arthropoda*, class *Crustacea*. Some plant species (such as tomatoes, lablab bean) show both types of growth, depending on environmental conditions or genetic variations.

This review is largely biased towards reviewing these qualitative growth types in different organisms. Some comments can be made on the definitions of growth patterns.

Is indeterminate growth never ending?

The definition of indeterminate growth may be confusing and may mislead to think that indeterminate growers never cease to grow. Certainly, nothing in nature can grow without limit. The maintenance of a larger body requires more energy, so the production of food and the capacities of organismal systems (e.g. respiratory, digestive) should increase accordingly. Sooner or later, various limitations will stop growth. Organisms in natural populations die early because they are subject to predation and environmental hazards. In favorable laboratory conditions, they usually live longer. Indeterminate growth, i.e. growth to which no end is observed during the natural lifespan, may stop if the organism had a chance to live longer. The main difference between the definitions is that indeterminate growth does not stop at, or soon after, reaching maturity, so organisms are able to increase their size-related reproduction capacity with time.

Determinate growth after sexual maturity

It is frequently mentioned in the literature that determinate growth stops at sexual maturity. The moment of sexual maturity is indeed a very important period in the life of every organism and a "turning point" in theoretical models of life history evolution. It cannot be regarded as a single age, because maturity is the result of complex developmental

processes that may take considerable time. In determinately growing organisms (such as humans), growth may not stop at the age of sexual maturity but continue for some time. For example, growth in humans does not cease entirely after sexual maturity is reached, but it does slow down significantly. By the time of sexual maturity, humans attain most of their adult height. Girls may add some height, as much as 5 cm, over the next two years. For boys, there is no such a clear end point, though there are also indications of full sexual maturity. Again, there may be some small additional growth in height after they reach this stage of development (see Figure 8).

Different parts of the organism can grow with different patterns
Consider a perennial long-living plant, a tree. The tree trunk constitutes the main, critical part of the tree; a serious damage to it will lead to death. The trunk grows indeterminately, gaining height and width, and acquiring rings. The roots also grow indeterminately to support the nourishment needs of the trunk and to provide stable support. Leaves, by contrast, grow at the beginning of each season, their growth is determinate and their size well defined. They provide the tree with photosynthesis and gas exchange. The leaves tear and wear and have no chance of surviving the cold season. So, at the end of the season, the tree removes water and nutrients from the leaves and sheds them. The cycle is repeated in the next season. Flowers and fruits of trees also grow determinately.

Growth, maintenance, and turnover
Living tissues age. In many cases, the lifespan of single cells is much shorter than that of tissues or the whole organism. To provide greater longevity, tissues undergo a constant process of turn-over, including the breaking-down of old and damaged components and the synthesis of new ones. Growth from the energetic, metabolic point of view may be considered as an excess of build-up over the break-down of tissues. This view was first proposed by Pütter (1920) and developed by Bertalanffy (1941, 1957) in his model of growth (see 3.3.1).

Many tissues in an adult human are renewed approximately every seven years; this corresponds to a synthesis of 13% of biomass yearly; the rate is comparable only to fast growth in childhood. So, it is not unrealistic to assume that turnover expenses, usually included in maintenance, are comparable to or greater than the expenses on growth itself.

2 Growth patterns in different phyla

We give examples of growth patterns for different phyla ranging organisms from more primitive to more complex. Specific features of growth are described in notes.

Table 1: Growth patterns in different phyla

Phyla	Determinate	Indeterminate
Kingdom *Protista*	Rhizopods (e.g. Amoeba (*Amoeba proteus*) (Prescott, 1957))	
Kingdom *Fungi*	Yeast (*Saccharomyces cerevisiae*, *Saccharomyces carlsbergensis*) (Berg and Ljunggren, 1982), most mushrooms	Hornwort
Kingdom *Plantae* [1]	Trees (leaves), lablab bean (*Lablab purpureus*), tomato (certain species, mostly early ripening), white lupin (*Lupinus albus L.*) (autumn-sown type) (Huyghe, 1997), soybeans (Robinson and Wilcox, 1998)	Trees (branches, trunks), perennial plants (primary bodies), roots, lablab bean (*Lablab purpureus*), tomato (certain species), white lupin (*Lupinus albus L.*) (spring-sown type) (Huyghe, 1997), soybeans (Robinson and Wilcox, 1998)
Kingdom *Animalia*		
Phylum *Cnidaria*	Hydra (Martínez, 1998)	Many benthic marine invertebrates (Sebens, 1977)
Phylum *Nematoda*	Nematode worm (*Caenorhabditis elegans*) (Lee, 2002)	
Subkingdom *Metazoa* Phylum *Annelida*		Segmented worm *Pristina leidyi* (Bely and Wray, 2001), (Dorresteijn and Westheide, 1999)
Phylum *Mollusca*	Snails (class *Gastropoda*), strombids (gastropods of the family *Strombidae*)	Long-lived freshwater bivalves, clams, freshwater mussels (Heino and Kaitala, 1999; Hanson et al., 1989; Jokela, 1997)
Phylum *Echinodermata*		Sea urchins (*Strongylocentrotus*) (Stephens, 1972; Gage and Tyler, 1985)
Phylum *Arthropoda* [2] Class *Insecta*	Insects with terminal moult, fixed number of instars (growth stages) – usually those with wings (most insects)	Insects with no terminal moult and no fixed number of instars (apterygote insects) [3]
Class *Crustacea*	Copepods (Kooijman, 2000), females of *Chionoecetes* crabs (Stone, 1999)	Cladocerans (e.g. *Daphnia magna*), males of *Chionoecetes* crabs (Stone, 1999) [4], lobsters [5] (Factor, 1995), crayfish, shrimp (Heino and Kaitala, 1999; Wenner, 1985)

Phyla	Determinate	Indeterminate
Phylum *Chordata*, Subphylum *Vertebrata*, fish[6]	Some fish species	Many species of teleost fish (Weatherley and Gill, 1987b), zebrafish (*Danio rerio*) (Kishi et al., 2003), *Brachyrhaphis rhabdophora* (*Poeciliidae* family)[7] and other poeciliid fish, salmonids (*Salmonidae*) – salmon, trout, Atlantic salmon (Grant et al., 1998; Purdom, 1993), Yellow perch (Huh, 1975; Malison et al., 1985)
Class *Reptilia*[8]	Blanding's Turtles (*Emydoidea blandingii*) (Congdon et al., 2001, 2003)	Painted Turtles (*Chrysemys picta*) (Congdon et al., 2001, 2003)[9], other tutrtles, snakes, lizards
Class *Aves* (birds)	All birds (Starck and Ricklefs, 1998; O'Conner, 1984)	
Class *Mammalia*[10]		
Subclass *Metatheria* (marsupials)	Female cangaroos	Males of Red, Eastern, and Western grey kangaroos (*Macropus giganteus*)[11], pademelons and parma wallabies (*Macropus parma*)[12]
Subclass *Eutheria* (placentals)	Rodents, Humans, (Kuczmarski et al., 2000; Tanner et al., 1998)	Males of American bison, giraffes, African and Indian elephants[13], mule deer, white-tailed deer (*Odocoileus virginianus*), black-tailed mule deer (*Odocoileus hemionus*)[14]

[1] Plants have some features not observed in animals, such as a modular body structure. Most plants have several phases of growth, complex patterns of seasonal growth, and different growth of different parts may be observed. Some plants show both types of growth, depending on environmental conditions or genetic variants. Determinate and indeterminate growth can be observed simultaneously in different parts of the plant, e.g. branches and leaves.

Plants exhibit two primary forms of flowering architecture (types of inflorescences): indeterminate and determinate. Species with indeterminate inflorescences have apical meristems that grow indefinitely, generating floral meristems from their periphery. In contrast, each apical meristem of determinate species is eventually transformed into a floral meristem that terminates apical growth, with subsequent growth occurring only from lower axillary meristems.

Determinate growth means that vegetation cedes development when flowering begins. The shoot meristems terminate by converting to a flower (e.g. tobacco and tomato) (Amaya et al., 1999). Indeterminate growth continues, adding leaf and stem tissue after blooming begins. Shoots grow indefinitely and only generate flowers from their periphery (such are *Antirrhinum* and *Arabidopsis*).

Plants, (perennials, at least) add to their primary bodies for as long as they live. While the ultimate basis for the indeterminate growth of plants is the iterative production of determinate units (morphological phytomers, cellular merophytes), there is no direct homology or equivalence between the determinate units and indeterminate units (shoot, root).

[2]The shell of insects and many crustaceans is hard and inelastic, for them growth is associated with molting – the cyclical process of shedding or ecdysis, a critical stage of development. Growth stages in insects are called instars.

[3]Although they also do not increase in size after a certain point.

[4]Growth patterns subject to debate.

[5]Molting is a continual process for them.

[6]Fish exhibit both types of growth and even gender change, and thus have the potential for a wide variety of reproductive behaviors and strategies (Gross, 1984). Most fish are indeterminate growers; they grow throughout their whole life with highly variable rates. Environmental factors and chance have a large impact on growth. The age of maturity is very plastic (Kooijman, 2000; Summerfelt and Hall, 1987; Weatherley and Gill, 1987a; Smith, 1992; Mommsen, 2001).

[7]In many species male growth slows dramatically at sexual maturation (Basolo, 2004). The growth curve nearly plateaus at advanced ages as maintenance costs and the allocation to reproduction increase.

[8]Undergo molting and grow in bursts.

[9]Turtles are often thought to exhibit indeterminate growth, but it appears that growth slows appreciably sometime after the onset of reproduction. Females are still growing rapidly during the first few years of reproduction.

[10]It is generally said that all mammals experience determinate growth, but they seem to experience both patterns. Male competition generally favors a bigger size, and in certain mammal species (cangaroos, elephants, deer) where such competition and the advantage of larger size are greater, evolution obviously resulted in the development of an indeterminate growth pattern in males. Size increase in older males is seen to act as a sexual attractant, signalling to females that males are long-lived and, therefore, desirable mates.

[11]The skeletons of kangaroos and the larger wallabies continue to grow slowly throughout life. Male kangaroos grow steadily larger and stronger throughout life, although at a decelerating rate as they age (Figure 1). The rate of growth in females begins to slow down at about two years of age and most are fully grown when they have reached the age of 5 years. The growth of kangaroos stops at some age, but far beyond the age of maturity (which is at about 2 years of age).The rate of weight increase in females is slower than that of males, but it is maintained until full size is reached at about ten years of age and there is, again, a tendency for a slight decrease in weight as the animals reach old age (Frith and Calaby, 1969; Dawson, 1994).

[12]In parma wallabies both females and males continue to grow after sexual maturity (age 1 year in females). At this age, they reach 70% of the maximum size (taken to be the size of animals aged 3 years and older). Growth measured by the length and weight ceases by age 3 years in females, but the arms and legs of males continue to grow until they reach about 4.5 years Maynes (1976).

[13]Elephants continue to grow for the entire duration of their life (Carey and Guenfelder, 1997; Elephant Encyclopedia, 2004; Lee and Moss, 1995; Haynes, 1991). Bulls (males) are sexually mature at about 11 to 12 years of age, but they typically are not allowed to mate until around age 30 years. Elephant cows (females) begin breeding at about 9 years of age. Elephants attain most of their height between the ages of 20 and 25 years, but continue to grow in height at a slow rate throughout life. Asian female elephants continue to gain weight long after puberty. The reproduction success related to mating competition is probably a factor that has influenced indeterminate growth at least in bulls. Lee and Moss (1995) argue that growth is indeterminate in male elephants and determinate in female elephants in the wild. Laws (1966) presents data on height and weight growth in elephants. Although the maximum (observed) size and weight for female and male elephants is defined, growth apparently continues throughout life and well after maturity. Growth in height continues at a diminishing rate and obviously has a limit, but it is usually beyond the common lifespan of the animal. Moreover, the tusks of male elephants continue to grow after puberty.

[14]The males of black-tailed mule deer grow after reaching sexual maturity, probably throughout all of their life. Typically, deer live between 8 and 11 years (the maximum recorded lifespan in captivity is 19 years). They reach sexual maturity between the age of 1.5 and 2.5 years and have a non-monotonic pattern of weight change (Figure 2) with prepubertal growth during the first half year of life and following seasonal oscillations with

an increasing year-average weight (Wood et al., 1962). The mean yearly mass increased in males after sexual maturity throughout the period of observation (1600 days) performed on several species of deer (Wood et al., 1962). The indeterminate type of growth in male deer can be attributed to competition, here, larger mass is advantageous. This is proven by the fact that males are not allowed to actively participate in the rut until they are three or four years old. Measuring growth in deer is complicated because the typical linear measures are difficult to undertake on living animals and weight may not be a good proxy to growth. The seasonal weight changes are largely due to the accumulation and disappearance of adipose tissue and annual increment in lean body mass (assumed to be represented by the lower weight limiting curve) is relatively small after puberty is reached (Wood et al., 1962). The predicted "terminal mature weight" (the maximum asymptotic weight) is delayed or never achieved.

Figure 1: **The change in size, measured by the total length along the contours of the body, and the total weight, male (solid line) and female (broken line) Red Kangaroos throughout life (mean measurements of 239 males and 964 females) (Reproduced from (Frith and Calaby, 1969)).**
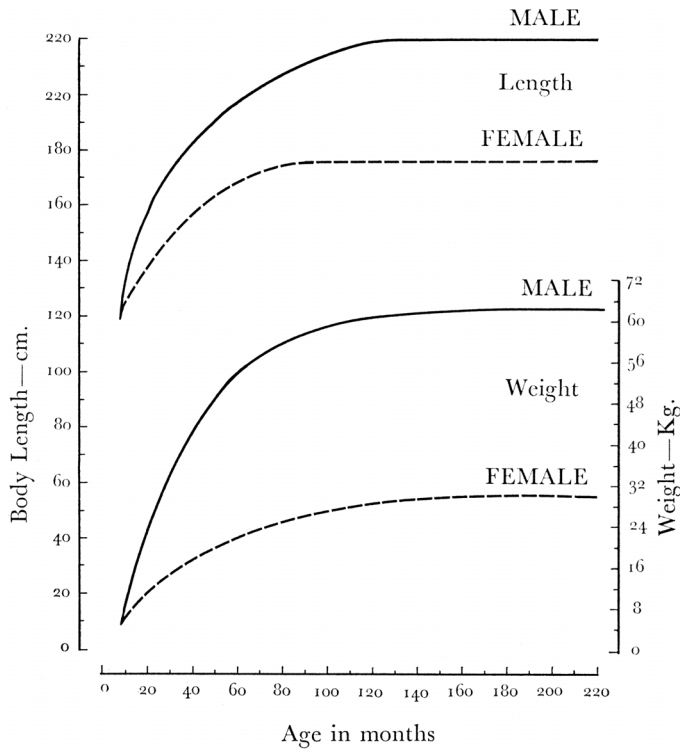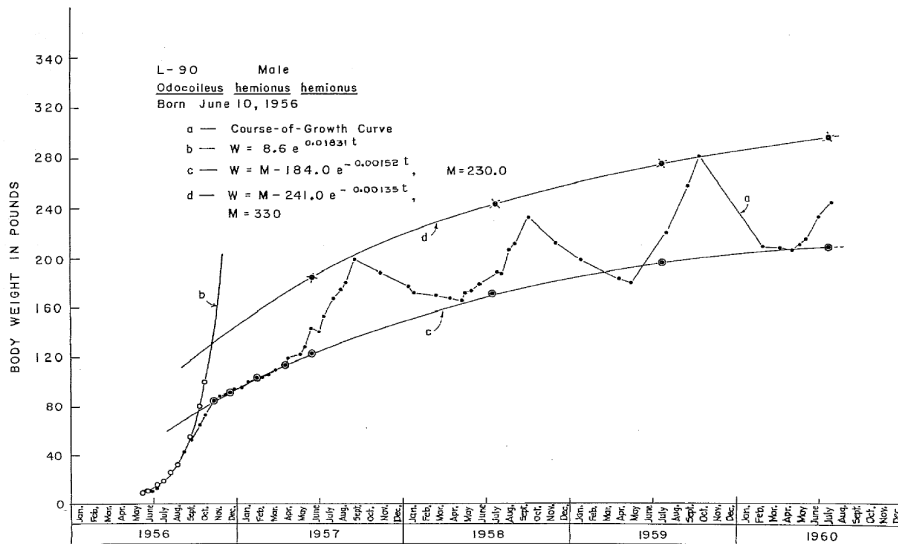
Figure 2: **Growth (life weight) for a representative male of black-tailed deer *Odocoileus hemionus*. Oscillating values of mass may be limited by curves of maximum and minimum year weights (Reproduced from (Wood et al., 1962) with permission from the Canadian Journal of Zoology).**

3 Mathematical description of growth

A convenient mathematical description of growth dynamics can be used to reduce the amount of measured data, explain observed patterns, compare growth rates and patterns within and between species, and to predict the future growth of these species. Two approaches have been used, namely descriptive growth curves and models based on theories of growth. Often terminologically not differentiated – both are called "growth models", the two approaches are quite different nevertheless. France and Thornley (1984) refer to these two types of description as empirical models set out principally to describe, and mechanistic models attempting to provide a description with understanding.

Growth curves as empirical models are parametric functions, with usually a few parameters relating to some measure of an organism's size and age. The mathematical functions of most growth curves do not reflect the nature and dynamics of the underlying biological processes. The growth curves are fitted to the data, and estimates of their

parameters are obtained. A wide range of questions on the growth of the organism can then be asked.

The main challenges stimulating the development of growth curves have been the detection of abnormal growth or disease at the early life stages in humans and the prediction and comparison of the growth of economically important animals, such as cattle, birds, and fish in order to find regimes of handling and harvesting that maximize product yield. The last problem has stimulated the development of models describing population growth, predator–prey interactions, and the coexistence of species.

A common application of growth curves in determinate growers is to establish an asymptotic size.

The great diversity of growth strategies observed in living organisms poses challenges in describing them in terms of a few simple curves. The goals of the structural approach to growth modeling are to find a suitable family of growth functions easily representing a set of longitudinal measurements, to estimate the growth parameters by fitting a function, to evaluate a goodness of fit, and to predict future growth.

Mechanistic models and theories of growth present a second, different approach – not just to fit the data but to develop a description of processes underlying growth that takes place in an organismal system. The models of growth can be simple and abstract, involving a simplistic description of build up and break-down of organism compounds and tissues, with each of these processes being related to size (model of Bertalanffy (1957)), or they may involve a detailed description of the balance of energy and compounds, the processes of consumption, an the storage and utilization of energy by different systems. Detailed models can take into account subtle processes such as changes in shape, dilution, the ratios of body reserves to somatic tissue, and the specifics of organism design and physiology, as in the Dynamic Energy Budgets theory (Kooijman, 2000).

A mechanistic model is usually derived from a differential equation relating growth rate (dy/dt) to size (y). This mathematical relationship represents the mechanism governing the growth process. This approach has been extensively used for somatic growth and a large number of growth functions have been derived, such as the monomolecular, logistic, and Gompertz ones (Turner et al., 1976; France and Thornley, 1984).

The purpose of mechanistic models and theories is to understand the similarities and differences in growth in different species and to explain these differences within one mechanistic framework. Equations of growth can be derived from these models.

Probably a more general approach to growth and generally, changes in size, would be to regard the organism's size as a result of a dynamic balance between the accumulation and break-down of biomass. Such concepts of dynamic turnover form the basis of the von Bertalanffy model and of the Dynamical Energy Budget theory.

3.1 Typically observed patterns of growth

Several patterns are frequently observed in the growth rates of freely fed organisms. The so called exponential pattern (Figure 3, unlimited dash-dot curve) is typical for growth in certain time periods usually soon after birth.

The asymptotic growth pattern which is also called exponential (Figure 3, leveling-off dash-dot curve) applies to the length of some organisms, the size of the skull and the brain. It is characterized by a positive and steadily decreasing growth rate, therefore there is no point of inflection.

The weight and volume of the body and of most organs show a sigmoid or S-shape growth pattern (Figure 3, line). Initially, the rate of growth in mass is low but increasing. The growth rate reaches a maximum, it corresponds to the point of inflection in the curve, and then slowly declines to zero when the animals achieve their mature weight. The sigmoid curve is prevalent among determinately growing animals, and this has led to the emergence of a specific class of "sigmoid functions" describing growth. A special case of this growth mode is multiphasic growth, where several sigmoid periods follow one another throughout the development and, therefore, several growth rate maxima are present (see the human growth curve in Figure 8).

Bell-shaped growth (Figure 3, dotted curve) is observed in organs that show degeneration and involution (thymus, bursa of Fabricius, bones in elderly humans, tree leaves at the end of the season). Organ size first increases and, after having reached a maximum, starts to decrease.

Growth can experience complex patterns, such as non-monotonic, oscillating changes in mass (e.g. in animals with strong seasonal differences in the quality of feed), and in perennial plants. Often, it is difficult to separate growth from the accumulation of resources when change in mass is the summary measure of these effects. As an example, the cyclic changes of mass due to the accumulation and utilization of fat in deer are overlayed on the monotonic growth of fat-free mass (see Figure 2). The growth pattern observed depends on the measure of growth selected – even in isomorphs the curves of growth in linear size and mass or volume will have different shapes.

For these patterns of growth, a multitude of growth curves has been proposed. None of them, however, meet the demands of a biophysical model in its narrow sense. Therefore, growth curve analysis is more or less a phenomenological analysis of growth courses.

3.2 Growth curves as empirical models

Growth curves can be classified according to the type of growth they describe: determinate or indeterminate. Most of the curves developed describe determinate growth, since this is what is most often observed in animals, most notably in mammals such as humans

Figure 3: **Frequently observed growth patterns: "exponential" (both dash-dot lines), sigmoid (line), and bell-shaped (dotted line).**
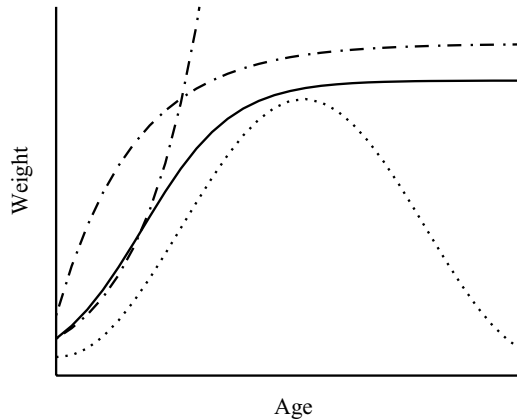
and cattle, which have been of primary interest. Since determinate growth is characterized by a maximum size that is approached with a diminishing growth rate, such curves are also called asymptotic. Examples are the exponential (with the declining growth rate), logistic, Richards, Gompertz, von Bertalanffy curves. All these curves except for the exponential have sigmoidal shape. In all following equations, t will denote the age of the individual, and $y = y(t)$ – its size.

3.2.1 Curves for determinate growth

The exponential growth curve
Assume that the rate of growth is proportional to the size: $dy/dt = by$. The solution of this differential equation defines the exponential growth curve

$$y = y_0 e^{bt}. \tag{1}$$

Parameter y_0 is the initial size (at age zero). For $b > 0$, this function will usually only be applicable to temporarily limited periods of growth (e.g. at the early growth stage) (see also the logistic growth curve (Figure 4)). For $b < 0$, this may be a good model of exponential decline, e.g. of some decaying activity.

Using a linear transformation of the form $\tau = -t$, $\tilde{y} = y_\infty(1 - y/y_0)$, "inverting"

time and size scales, we obtain a variant of the exponential growth curve which allows for an asymptotic approach to the maximum size y_∞:

$$\tilde{y} = y_\infty(1 - e^{-b\tau}), \tag{2}$$

This form of curve is often referred to as the von Bertalanffy curve, but note that the actual solution (20) for the von Bertalanffy model (19) has the form of an exponential function (1) raised to the power $1/(1-m)$. For animals, typically $2/3 < m < 1$ so $1/(1-m) > 3$. Equation (2) can also be written in the form of $y = y_\infty(1 - e^{-k(t-t_0)})$, where t_0 is the theoretical age at which the organism would have zero size. k is often called the Brody growth coefficient, or the rate at which y_∞ is achieved or a measure of the rate at which the growth rate declines. Brody himself used this type of "inverted" exponential growth function in the second part of his sigmoidal functions (6, 7). Generally, a high k is associated with fast early growth, low age and size at maturity, high reproductive output, a short life span, and a short max length. The exponential curve of this form is a particular case of monomolecular growth, in which the rapid initial growth is followed by a leveling off.

The exponential curve can be applied to mass as well as to length. It fits length better than mass and works better for older ages. During larval and early juveniles stages, a sigmoid curve is more applicable.

Monomolecular growth

One of the simplest assumptions leading to a growth curve approaching a limiting value y_∞ is that the growth rate is proportional to the difference between the level and the actual size, i.e. $dy/dt = b(y_\infty - y)$, where $b > 0$. The solution to this differential equation is the monomolecular growth function:

$$y = y_\infty - (y_\infty - y_0)e^{-bt} = y_\infty - \delta e^{-bt}, \tag{3}$$

Here, y_0 is the initial size and if $y_0 = 0$, the solution reduces to $y = y_\infty(1 - e^{-bt})$, a special case (2) of exponential growth curve. The monomolecular curve has rapid initial growth followed by a leveling off.

Logistic growth

Qualitatively, the growth of an animal can be divided into four stages: early exponential growth, where the rate of growth is proportional to weight; linear growth, where more and more energy is devoted to maintenance; diminishing growth as a maintenance balance is approached; and antithesis through senescence. The last part is often disregarded since few or no observations are made at this stage or since it is irrelevant to consider this stage. The growth rate at the first stage is proportional to the weight of the animal: $dy/dt = by$.

The solution of this differential equation is exponential growth (1). Growth at the second stage is linear in time, i.e. $y = y_0 + bt$. The third stage is a limiting stage, where the growth rate approaches zero and the weight approaches a limiting level y_∞. The fourth stage will not be considered here. By considering the first three stages only, the growth can be described by a differential equation: $dy/dt = by(y_\infty - y)/y_\infty$. The solution to this is known as the logistic curve

$$y = \frac{y_\infty}{1 + e^{\eta - bt}}. \tag{4}$$

The size, y, approaches the upper limit y_∞ as time tends to infinity. The parameter η has no direct interpretation but may be seen as a measure of the difference in weight from birth to maturity since isolating η at time $t = 0$ and letting $\alpha = y_0$ we find that $\eta = \ln(\eta/\alpha - 1)$. Inserting this result into the equation of the logistic curve (4), we can write the following re-parameterized version:

$$y = \frac{\alpha y_\infty}{\alpha + (y_\infty - \alpha)e^{-bt}}. \tag{5}$$

This way of expressing the logistic curve has the advantage that the initial weight is a parameter in the model. The logistic curve (Figure 4) is sigmoid, has a lower limit at 0, and an upper limit at y_∞. The curve is symmetric around the point of inflexion $y = y_\infty/2$ where the absolute growth rate is maximal. The last property is one of the drawbacks of the logistic growth curve. The Gompertz growth curve is more flexible.

The Sigmoid (Brody) curves
As mentioned, sigmoid patterns of growth are frequently observed in animals that are determinate-growers. Brody (1945) suggested growth be expressed by a continuous curve with a discontinuous slope at the inflection point – the sigmoidal curve, often referenced to as Brody's curve. He described growth as "self accelerating" before and "self inhibiting or decelerating" after age t', and suggested the following mathematical description:

$$y = y_0 e^{bt}, 0 \le t \le t', \tag{6}$$

$$y = y_\infty \left[1 - e^{-k(t - t^*)} \right], t \le t \tag{7}$$

Here, y_0 is the initial live weight of the animal (i.e. the weight at birth), b is the exponential growth constant in the growth acceleration phase, y_∞ denotes the mature live weight, k represents the exponential growth rate decay constant in the deceleration phase, and t' is the point of inflection (the age at which acceleration of growth turns into deceleration), and t^* denotes the time-shifting parameter. The curve defined by Equations (6, 7) fits the

Figure 4: **Logistic growth curve** $y = \frac{a}{1+ce^{-bt}}$.
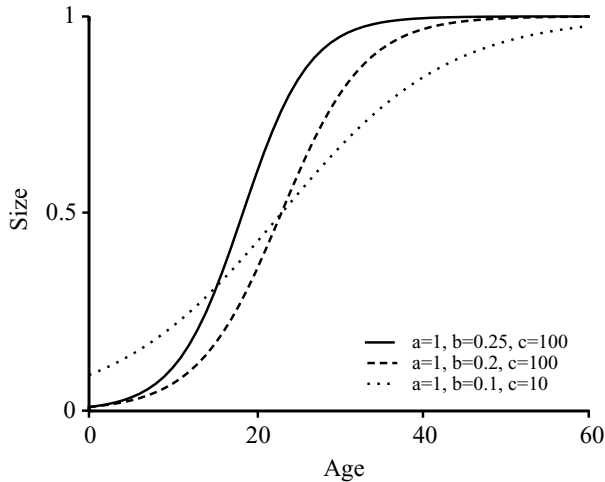
growth data for many animals very well. This motivated Brody to call the parameters y_∞, k, and t^* genetic "constants", and to create an extensive table listing the values (Brody, 1945; Parks, 1982).

Brody suggested to express growth in coordinates of the degree of maturity ($\mu = y/y_\infty$) versus normalized age T, using transformations $T = k(t - t^*)$ and $u = 1 - e^{-T}$, $0 < T$, and demonstrated that the growth data for a wide range of animals lie on the same graph (Figure 5). The coincidence of the growth data from such widely differing species for $T > 0$ is remarkable. A plot in these coordinates shows where the determinate growth of different animals has the same features and where it differs (Parks, 1982).

The Richards curve

Richards (1959) was the first to apply to the plant sciences a growth equation developed by von Bertalanffy to describe the growth of animals (France and Thornley, 1984). The Richards curve is very general and has the monomolecular ($\nu = -1$), the logistic ($\nu = 1$), and the Gompertz ($\nu = 0$) curves as special cases, where ν is a parameter in Richard's equation. As with the other growth curves, there are various ways of writing the curve equation. One of them (Labouriau et al., 2000) is:

$$y = \alpha\{1 + sign(\nu)e^{\beta-\kappa t}\}^{-1/\nu}. \tag{8}$$

Here, α, $\beta > 0$ and $\nu \geq -1$ but $\nu \neq 0$ (for $\nu = 0$ the Gompertz equation is used), and

Figure 5: **Growth in rats, cows and man expressed in Brody's normalized age T and fraction of maturity μ (Reproduced from Parks (1982)).**
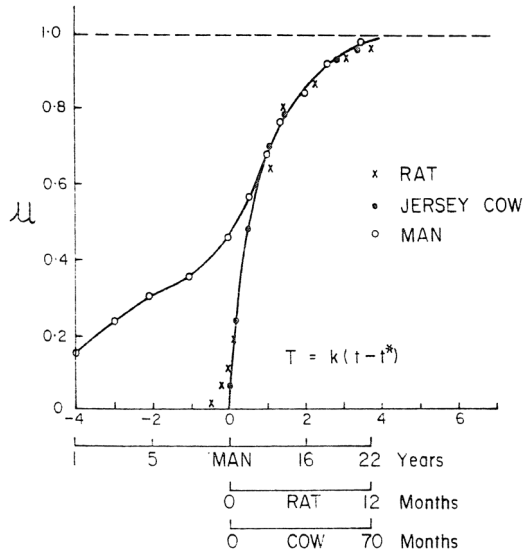
$sign$ is a signum function ($sign(x) = -1, x < 0, 0, x = 0$ and $1, x > 0$). The curve has an inflection point at the time point $t = (\beta - \ln(|\nu|))/\kappa$. The expected response at the inflection point is given by $\mu = \alpha(\nu + 1)^{-1/\nu}$.

The point of inflection now is able to occur at any fraction of the final weight, as ν varies over range $-1 \leq \nu < \infty$. Parameter κ controls the position of the inflection point. The intercept (the value at t=0) of the Richards curve is

$$y_0 = \alpha \left\{ 1 + sign(\nu)e^{\beta} \right\}^{-1/\nu}. \tag{9}$$

Parameter α is the limiting size (the asymptote of the curve). Parameter ν determines the relative value (compared to the limiting size) of the Richards function at the inflection point:

$$\frac{y}{\alpha} = (\nu + 1)^{-1/\nu}. \tag{10}$$

Parameter β controls the initial size. Other forms of equations defining the Richards curve are $y = d + a/\{1 + ce^{-b(t-m)}\}^{(1/c)}$, where a is the maximum asymptotic size,

http://www.demographic-research.org

Figure 6:   **Richard's growth curve** $y = d + a \left\{ 1 + ce^{-b(t-m)} \right\}^{-1/c}$.
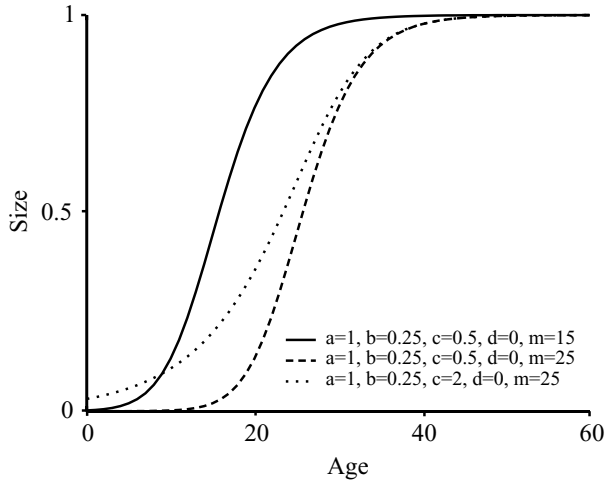
d the lower asymptotic size, b denotes the average growth rate, m the age of maximum growth, c determines whether max growth occurs early or late, and $y = \alpha\{1 - \beta_1 e^{-\beta_2 t}\}^{\beta_3}$. In practice, the Richards curve is rather difficult to fit due to numerical problems. The model has too many parameters for practical situations and is an example of over-parametrization.

The Gompertz growth curve

The Gompertz equation arises from models of self-limited growth where the rate decreases exponentially with time. The model was first introduced to describe growth in the number of tumor cells which usually follows a sigmoidal growth pattern. The equation is a solution of the differential equation:

$$\frac{dN}{dt} = \lambda N \ln(\theta/N); \quad N(0) = N_0, \tag{11}$$

where N is the number of tumor cells at time t.

Let the growth rate be expressed by the differential equation $dy/dt = kye^{-bt}$, where b and k are constants. The solution is

$$y = y_\infty e^{-(k/b)e^{-bt}}, \tag{12}$$

where y_∞ is the asymptotic size. Alternatively, the growth rate may be defined by a differential equation of the form $dy/dt = y(\beta - \alpha \ln y)$, where α and β are constants. The solution of this equation is:

$$y = e^{C_1(e^{-\alpha(t+C_2)}+\beta)/\alpha} \tag{13}$$

Figure 7: **The Gompertz growth curve** $y = ae^{-ce^{-bt}}$.
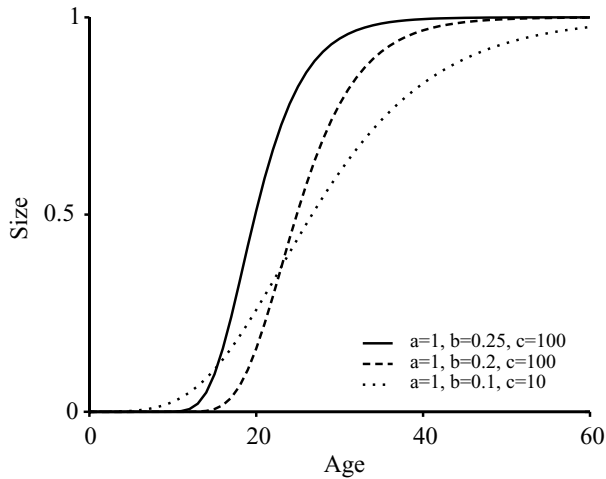
Solutions of these models are know as the Gompertz growth curve, which is usually expressed in the form

$$y = y_\infty e^{-ce^{-bt}}, \tag{14}$$

where $y_\infty > 0$ is the final (asymptotic) size, parameter $b > 0$ describes the decay in the specific growth rate, and parameter $c > 0$ controls the difference between the initial and final weight. The point of inflection is the time point where $y = y_\infty/e$, this gives $t = (\ln c)/b$. The Gompertz curve allows for asymmetry around the inflection point, and reaches the point of inflexion before 50% of the maximum size is reached. It is frequently used in biology to describe individual growth in length, the growth of populations, and the growth of tumors (Savageau, 1980). Compared to logistic growth, the Gompertz curve shows faster early growth, but a slower approach to the asymptote, with a longer linear period around the inflection point. The initial values can be found via a transformation

known as the log-log link function: $\ln(-\ln(y/y_\infty)) = \ln c - bt$. Asymmetry can be inverted by applying an exponent to both parts: $y = y_\infty(1 - e^{-ce^{-bt}})$, this is known as the complementary Gompertz curve. Again, the initial values can be found by a transformation known as the C-log-log link function: $\ln(-\ln(1 - y/y_\infty)) = \ln c - bt$.

The Gompertz growth model should not be confused with the Gompertz model of mortality, $\mu(t) = ae^{bt}$, introduced by Gompertz (1825) to describe increase of mortality, μ, in adult humans with age. It is well known in mathematical demography.

The von Bertalanffy curve

Bertalanffy (1941) proposed the first model of animal growth based on metabolic processes (20). It will be discussed in section 3.3.1. The solution of this model, and more generally, asymptotic growth curves of the form

$$y = y_\infty - (y_\infty - y_0)e^{-ct} \tag{15}$$

are referred to as the "von Bertalnaffy" growth curves and widely used to describe growth in animals and humans. This is a case of asymptotic growth from initial size y_0 to asymptotic size y_∞ with a decreasing rate. The curve has no inflection point.

3.2.2   A curve for indeterminate growth

Curves with upper limits cannot be used to describe indeterminate growth. The exponential growth curve increasing monotonously is too rough to use. Tanaka (1982) introduced a four-parameter curve for indeterminate growth that has an initial period of exponential growth followed by an indefinite period of slow growth. It was the first model that reasonably described indeterminate growth. The function, which he named ALOG, has the form:

$$y = \frac{1}{\sqrt{f}} \ln\left(2f(t - c) + 2\sqrt{f^2(t - c)^2 + fa}\right) + d, \tag{16}$$

where $a > 0, c, d > 0$, and $f > 0$ are parameters. The curve monotonously approaches infinity as t increases. The growth rate is $dy/dt = 1/\sqrt{f(t - c)^2 + a}$. It is positive over all range and reaches a maximum at $t = c$ (the inflection point), therefore the growth curve has a sigmoid shape near c. The growth curve was first applied to data on spoon shell *Laternula anatina* and *Theora lubrica* (Tanaka and Kikuchi, 1979, 1980).

3.2.3   Multiphasic growth curves

Growth trajectories of animals demonstrate several periods of rapid growth (growth bursts) – human growth is an example of such a pattern (Figure 8). Such growth can be described

best by a combination of separate growth curves for each period. Koops (1986) proposed to use a multiphasic growth curve formed as a summation of several (n) logistic growth functions. Human height growth curves of this type are known as "double logistic" ($n = 2$) and "triple logistic" ($n = 3$) growth curves (Bock and Thissen, 1976). He noted that there is evidence for the existence of growth phases in the weight growth curves of animals. The fit of the multiphasic growth curve, applied to pika, mice, and rabbit weights, was shown to be superior to the monophasic model in terms of residual variances and the absence of the autocorrelation of residuals.

3.2.4 Polynomial growth curves

The use of polynomials to represent growth curves has been accorded high importance by many researchers (Goldstein, 1979; Wishart, 1938) since polynomials can approximate any curve. In this sense, polynomial curves have certain advantages over other types of curves. Polynomials are simpler to fit, and it is also easier to work out the statistical distribution properties of the parameters when fitted to a sample of individuals than in the case of curves such as the logistic one (Goldstein, 1979). Sandland and McGilchrist (1979) described and fitted the third degree polynomial model using a stochastic approach to the preadolescent human height data.

Yi and Li-feng (1998) introduced a model based on the Gompertz and polynomial model:

$$y = ce^{\sum_{i=0}^{n-1} \alpha_i t^i}.$$
(17)

Hasani et al. (2003) introduced a type of polynomial model of order n to fit growth data during infancy:

$$y = \alpha_0 + \sum_{k=1}^{n}\{(-1)^{k+1}\alpha_k \frac{t^k}{c^k}\},$$
(18)

They described how to select the order of the model and used the model of order 6 to fit the data set on US children.

For a mathematical entrance to the subject of growth curves, refer to (France and Thornley, 1984, ch. 5). Moreover, (Draper and Smith, 1981, ch. 10), (Mead et al., 1993, ch. 12), and many other textbooks consider growth curves.

3.2.5 A description of human growth

Human growth (Figure 8) is determinate and characterized by two points of inflection – around birth and around the point of sexual maturity. To fit growth data for certain age

intervals, usually early childhood, several curves have been proposed. The model of von Bertalanffy (see 3.3.1) is widely used to describe growth in animals and humans. Jenss and Bayley (1937) suggested one of the early curves of human growth in height during childhood in the form of $y = a + bt - e^{c-dt}$. The curve is a combination of the von Bertalanffy's growth curve and the linear growth curve. Count (1943) introduced a curve for growth patterns in human height in the form of $y = a + bt + c\log(t)$. Jolicoeur (1963) introduced a multivariate allometry model. Krüger (1965) proposed the so-called Reziprok function. Tanaka (1976) suggested the double exponential curve. Bock and Thissen (1976) introduced a triple logistic model to describe human growth in height to adulthood. Thissen et al. (1976) proposed a two-component model for individual growth and tested the model by comparing the patterns of growth in the stature of subjects from the four major U.S. longitudinal growth studies. He described problems comparing data from independent growth studies and offered solutions. Preece and Baines (1978) introduced a new family of mathematical functions to fit longitudinal growth data. All members derive from the differential equation $dh/dt = s(t)(h_1 - h)$, where h_1 is the adult size and $s(t)$ is a function of time. The form of $s(t)$ is given by one of many functions, all solutions of differential equations, thus generating a family of different models. Shohoji and Sasaki (1987) modified and extended Count's model to $y = a + bt + c\log(1 + dt)$. In 1989 Nelder introduced a modified logistic model and Jolicoeur and Pontier (1989) introduced a generalization of the logistic model. An asymptotic lifetime growth model of height was introduced by Kanefuji and Shohoji (1990) by modifying a fundamental growth model considering a relative measure of maturity. This model, compared to the previous model of Preece and Baines (1978) and the (Jolicoeur et al., 1991, 1992) (JPA1), was the best considering the goodness of fit. Jolicoeur et al. (1992) proposed an improved version of the JPA1 model which is a modified version of the JPA1 model and the triple logistic model of Bock and Thissen (1976). The new model is called the JPA2 model.

The curves most commonly used today in studies on humans growth and development are the Gompertz model, the triple logistic model of Bock and Thissen (1976), the modified logistic model of McCullagh and Nelder (1989), a generalization of the logistic model by Jolicoeur and Pontier (1989), the Preece and Baines (1978) model, the modified version of the Shohoji and Sasaki (1987), the model of Kanefuji and Shohoji (1990), JPA1 (Jolicoeur et al., 1991, 1992), the model of Jolicoeur et al. (1988) for human growth in childhood, the latter which is widely used and referenced to as JPPS, and especially JPA2 models.

Jolicoeur et al. (1991) tested the performance of several widely used growth models applied to human growth and found the JPPS to be the most satisfactory asymptotic model for growth in human stature. The further development of growth curves has led to the introduction of multiphasic curves which fit different phases of a complex growth patterns

Figure 8: **Human growth. a) body mass from conception to the age of 20; b) length of foetus from conception to birth / mean length of a baby (0 – 2 years) / stature of boys (2 – 20 years); birth occurs at age $t = 0$. Data on foetus development for USA children from (MedlinePlus Medical Encyclopedia, 2006; Moore and Persaud, 1998), post-birth data for USA boys from (Kuczmarski et al., 2000). The curves are not continuous due to merging of data from the sources and the use of different methods of length measurement for different ages.**
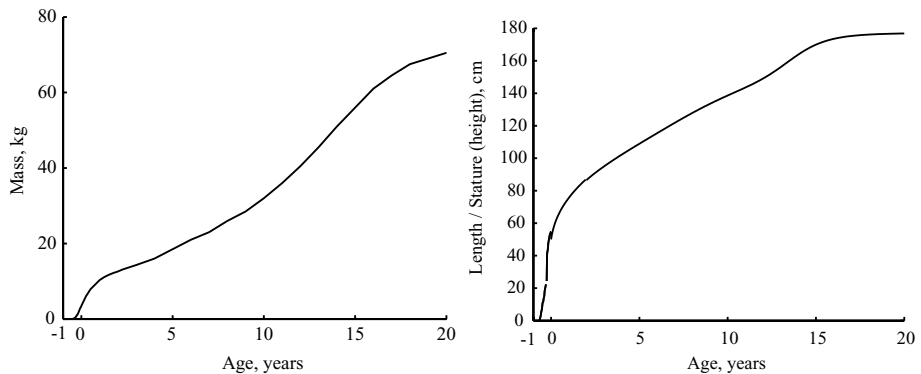
by separate curves with different parameters (see 3.2.3), and finally to polynomial curves (see 3.2.4).

Recent studies have found a positive relationship between stature and reproductive success of men in contemporary populations (Pawlowski et al., 2000; Mueller and Mazur, 2001; Nettle, 2002a). This appears to be due to their greater ability to attract mates. The study of Nettle (2002b) examine the life histories of a British women and found height to be weakly but significantly related to reproductive success. The relationship was U-shaped. This pattern was largely due to poor health among extremely tall and extremely short women.

Humans demonstrate evident sexual dimorphism – in length measurements the difference amounts to about 10%. Hypotheses proposed to account for sexual dimorphism in body size include sexual selection due to competition for mates in polygynous species; different "habits of life" of sexes and incidental selection of genes for larger body size. The extent of dimorphism varies between populations. This was attributed to greater susceptibility of male growth to nutritional deficiencies; different ecological niches (foraging strategies) of sexes; correlation between production of a certain sex in a certain society and parental investment in children of that sex; sexual selection, leading to bigger

men in populations with polygynous marriage because of intra-male competition for females, and interaction between female size and probability of birth-related complications (Rogers and Mukherjee, 1992; Guégan et al., 2000). Male and female weights are tightly correlated and dimorphism is not a simple allometric function of size. Lindenfors and Tullberg (1998) studied the relationship between primate mating system, size and size dimorphism.

3.2.6 A description of cattle growth

The description of growth in cattle has a purpose similar to that in humans – detecting early deviations in development, future growth, and the projection of the final size of the animal. Several classical equations have often been used to describe growth patterns and predict growth in cattle, and several new ones have been specifically developed: the Gompertz equation (mass) and the logistic (mass), the Brody, the von Bertalanfy (length), Feller, Weiss and Kavanau, Fitzhugh, Richards (variable), Laird, and Parks equations, and the Tanaka equation (though it was created for indeterminate growth). Summarized descriptions can be found in (Arango and Van Vleck, 2002; Parks, 1982). See also (Brown et al., 1976; Fitzhugh Jr., 1976; Johnson et al., 1990). Parks (1982) covered various aspects of describing cattle growth and proposed his own synthetic growth model. Recently, another model of cattle growth was proposed by (Hoch and Agabriel, 2004a,b).

3.3 Theories and mechanistic models of growth

3.3.1 A model of von Bertalanffy

The relation of the metabolic rate to body mass in different species has been discussed for several decades. Pütter (1920) indicated that animal growth be considered the result of a balance between synthesis and destruction, and between anabolism and catabolism of the building materials of the body. The organism grows as long as building prevails over breaking down; the organism reaches a steady state if and when both processes are equal.

Von Bertalanffy devoted large efforts to the study of individual growth (Bertalanffy, 1951). He noted that the metabolic rate in different species scales in different relation to mass, M, and divided the animal species into three groups. In the first, the metabolic rate scaled as $M^{2/3}$ in accordance to the "surface rule" (Brody, 1945; Kleiber, 1947; Krebs, 1950); in the second it was proportional to M; and the third group had intermediate levels. Interestingly, different metabolic types corresponded to different growth types (Table 2). "It appears that it is possible to establish a *strict connection between growth types and metabolic types* with respect to dependence of the metabolic rate on the body size", as Bertalanffy (1951) noted.

Table 2: Metabolic types and growth types. Growth is measured as increase in linear size. Modified from (Bertalanffy, 1951).

Metabolic type	Growth type	Examples
I. Respiration surface-proportional	(a) Linear growth curve: attaining *without inflexion* a steady state. (b) Weight growth curve: *sigmoid*, attaining, with inflexion at c. $1/3$ of final weight, a steady state	Lamellibranchs, fish, mammals (disputed; true at least in rats), certain invertebrates (isopod crustaceans, mussels, Ascaris)
II. Respiration weight-proportional	Linear and weight growth curves *exponential,* no steady state attained, but growth intercepted by metamorphosis or seasonal cycles	Insect larvae, *Orthoptera*, *Helicidae* land snails, hemimetabolic insects, Annelids (e.g. earth worms)
III. Respiration intermediate between surface and weight proportionality	(a) Linear growth curve: attaining *with inflexion* a steady state. (b) Weight growth curve: *sigmoid*, similar to I(b)	*Planorbidae* (pond snails), *Limnaea*, Planarians

Bertalanffy (1941, 1942) proposed the first model of animal growth based on metabolic processes and Pütter's idea of balance between the processes of catabolism and anabolism in the form

$$dM/dt = \eta M^m - \kappa M^n, \tag{19}$$

where changes in body mass, M are given as difference between the processes of building up and breaking down; η and κ are constants of anabolism and catabolism respectively, and the exponents m and n indicate that the latter is proportional to some power of the body mass. The solution of the differential equation (19) (for $n = 1$) is

$$W = \{\eta/\kappa - [\eta/\kappa - W_0^{(1-m)}]e^{-(1-m)\kappa t}\}^{\frac{1}{1-m}}, \tag{20}$$

where W_0 is the weight at time $t = 0$ (Bertalanffy, 1957). This growth curve is frequently used to describe animal growth and referred to as the "von Bertalanffy" of "Brody–Bertalanffy" growth curve because it resembles the inverted exponential growth function used by Brody in his sigmoidal function. It is the first growth curve specially designed to describe an individual. The curve has been proposed for animals, but is widely used for humans, too.

Bertalanffy (1951) classified the growth patterns observed in animals according to their metabolic features. He questioned the relation between metabolism and size (Bertalanffy and Pirozynski, 1951), and studied the intra- and interspecies allometry (Bertalanffy and Pirozynski, 1952) and the quantitative aspects of growth in relation to the metabolism (Bertalanffy, 1957).

3.3.2 The theory of growth of Turner et al.

There have been many contributors to kinetic theories of growth, such as Verhulst (1838), Pearl and Reead (1920), Medawar (1940), Bertalanffy (1941), Lotka (1956), Bertalanffy (1957), Richards (1959), Nelder (1961), Quetelet (1968) and Turner et al. (1969). The early history of the subject was reviewed by Glass (1967).

Turner et al. (1976) presented a generalized theory of growth based on three postulates. The first asserts that the rate of growth is jointly proportional to the monotonic function of the generalized distance from the initial size to the present size ("reproductive capability"), and to a monotonic function of the generalized distance from the present size to the ultimate size ("the limiting factor"). The second postulate restricts the monotonic function to power (or "mass action") functions. The third postulate constrains the model to a mathematically tractable set that nevertheless is sufficiently general to include the Malthusian, Gompertz, logistic, and con Bertalanffy-Richards growth models.

On the basis of these postulates they obtained a generic growth function that has as special limiting cases several well-known growth curves such as the Verhulst logistic curve, the Gompertz curve, and the generalized growth curve of von Bertalanffy and Richards. In addition, they obtained several new forms. The relation between their growth curve and other well-known growth curves is shown in Figure 9. The most general case is termed by Turner et al. (1976) the "generic growth model". Other special cases are termed "hyperGompertzian" and "hyperlogistic growth".

3.3.3 Park's theory of animal feeding and growth

Parks (1982) analyzed a large number of sets of experimental growth and feeding data for cattle and domestic animals on various diets and under various feeding regimes, and looked for deterministic elements in animal feeding and growth patterns that could form the basis of a testable theory. He integrated these studies into a mathematical theory of feeding and growth, allowing to predict animal growth under different feeding regimes. The theory is related to the laws of energy balance. Parks' theory is sufficiently robust to be used in studies on the diet and nutrition of other growing animals. He illustrated the applicability of his theory in a long-term experiment on two genotypes of chicken and discussed the implications of the theory in genetic experimental work on bending the growth curves of mice and chicken by selection techniques and in the economics of intensive animal productions.

3.3.4 The theory of Dynamic Energy Budgets of Kooijman et al.

Dynamic Energy Budget (DEB) theory goes far beyond the description of growth and quantifies the energetics of individuals as it changes during life history. The key processes

Figure 9: **The interrelation between the growth curve of Turner et al. (1976) and other well-known growth curves (Reprinted from Math. Biosci. 29, Turner, M., E. Bradley, K. Kirk, and K. Pruitt A theory of growth pp. 367-373, Copyright 1976, with permission from Elsevier).**
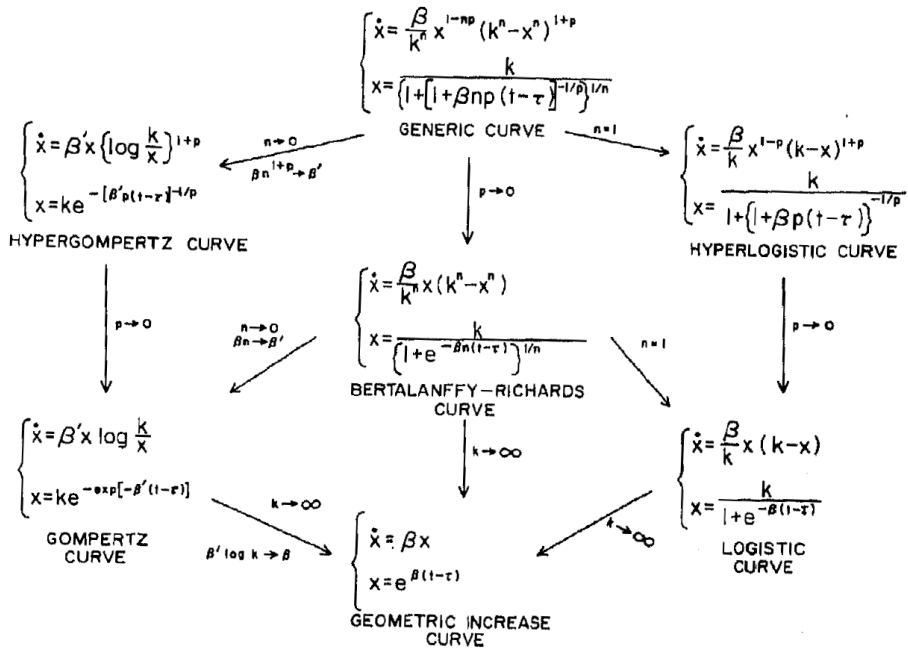
are feeding, digestion, storage, maintenance, growth, development, reproduction, product formation, respiration, and aging. The theory amounts to a set of simple mechanistically inspired rules for the uptake and use of substrates (food, nutrients, light) by individuals. It has far-reaching implications for population dynamics and metabolic organization. The theory explains the dynamics of only one variable, size (i.e. growth).

The theory was developed in (Kooijman, 1986b,a; Lika and Nisbet, 2000; Nisbet et al., 2000; Kooijman, 2001) and published in complete form in (Kooijman, 1993, 2000). It was tested against data (Zonneveld and Kooijman, 1989; Noonburg et al., 1998), applied to structured populations (Kooijman et al., 1999), to the growth of tumors (van Leeuwen et al., 2002, 2003), to problems of allocation to growth and reproduction (Lika and Kooijman, 2003); many other examples of application are given in the book. DEB theory predicts that an isomorph follows the von Bertalanffy growth curve at abundant food and

that the von Bertalanffy growth rate is (approximately) inversely proportional to the maximum volumetric length. This is shown for data on 261 widely different species. The DEB theory results in some well known empirical models for special cases and, therefore, has considerable empirical support.

3.3.5 The general model of ontogenetic growth of West et al.

West et al. (2001) proposed a general quantitative model based on fundamental principles for the allocation of metabolic energy between the maintenance of existing tissue and the production of new biomass. They derive the values of the parameters governing growth from basic cellular properties and construct a single parameterless universal curve that describes the growth of many diverse species (Figure 10). The model provides the basis for deriving allometric relationships for growth rates and the timing of life history events (Charnov, 1993; Peters, 1983; Calder III, 1984).

3.4 Selecting the growth model

Many growth curves have been proposed to describe growth in humans and animals. Some curves were proposed specifically to fit human data and cattle data. Most curves and models of growth describe linear growth (in length or height), other better fit the dynamics of mass.

Growth functions have certain mathematical limitations that need to be considered when choosing an appropriate model. For example, if a function does not have a point of inflection, the result of fitting will yield none even if the data show it.

Some functions were constructed to describe a specific stage of growth. For example, many functions proposed for a specific interval of rapid growth (infancy) in humans are unlimited and cannot be applied to the whole life period of the determinate grower.

A specific growth curve is sometimes chosen by simply looking at the plots of the data. Sometimes it is preferable to select or construct a function that has a biological interpretation and meaningful parameters. The functional relationship in the growth models is often derived from knowledge on the rates of growth dy/dt typically as a solution of a differential equation.

The choice of the most suitable model is a tradeoff between flexibility and complexity. For example, the logistic model and the Gompertz curve are simple and perform well in practice even on short series. The Richards model is complex, has many parameters and can fit complex patterns but it is difficult to fit and needs long time-series of good data. In some experiments it was reported to not converge or to produce biologically meaningless parameter estimates.

Figure 10: **Universal growth curve. A plot of the dimensionless mass ratio,**
$r = 1 - R \equiv (m/M)^{1/4}$**, versus the dimensionless time variable,**
$t = (at/4M^{1/4}) - \ln[1 - (m_0/M)^{1/4}]$**, for a wide variety of**
determinate and indeterminate species. When plotted in this way, the
model of West et al. (2001) predicts that growth curves for all
organisms fall on the same universal parameterless curve $1 - e^{-t}$
(shown as a solid line). The model identifies r **as the proportion of**
total lifetime metabolic power used for maintenance and other
activities (Reproduced by permission from Macmillan Publishers
Ltd: Nature West, G. B., J. H. Brown, and B. J. Enquist (2001). A
general model for ontogenetic growth [Letters to Nature]. Nature 413,
628-631, copyright 2001).
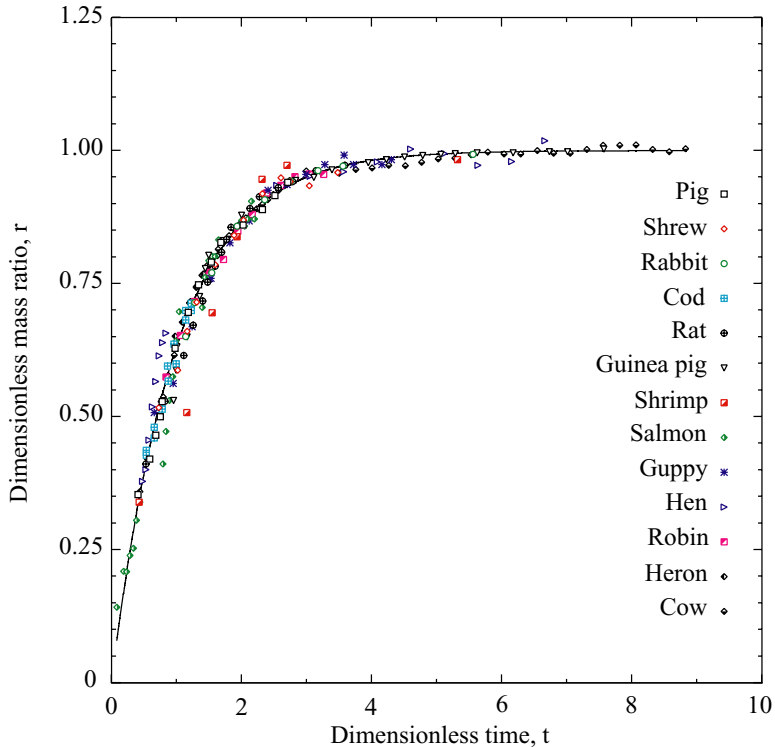
The process of constructing growth curves is an ongoing process driven by the aim to create a parametric function (producing a family of growth curves) with a minimum number of parameters and the best fit to the growth data of a given organism and growth period. When several models are being compared the quality of fit is considered in the sense of some criteria, such as the Akaike Information Criteria (AIC) (Akaike, 1972) which allows to account for a different number of fitted parameters.

Data for determinate growth in length (or mass$^{1/3}$) often is well fitted by the von Bertalanffy growth curve (Kooijman, 2000). The most frequently used growth curves also include the Gompertz and sigmoidal logistic curves (Tanaka, 1982). The exponential growth curve (Brody, 1945), the Reziprok function (Krüger, 1965), and the double exponential curve (Tanaka, 1976) also have been used sometimes as growth curve. Except for the exponential curve, these curves increase monotonically with age and converge to a finite value.

Zullinger et al. (1984) tested the fit of the von Bertalanffy, Gompertz, and logistic sigmoidal growth curves to data on the maximum of 331 mammal species in 19 orders; most data was obtained from longitudinal studies on captive animals. The best fit on a sample of 49 species was provided by the von Bertalanffy and Gompertz equations. The authors discuss the problems of fitting mammalian growth data and list the parameters of the Gompertz growth function for data from 331 species. They also provide references to the original data. Heppell et al. (2000) gives a list of available life tables for 50 mammal populations. More information on growth in mammals can be obtained from (Vaughan et al., 2000).

4 A comparison of growth between species

4.1 Allometry and scaling relationships

The relationship of body size to the anatomical, physiological, behavioral, and ecological characteristics has since long been a focus of interest in zoology. As one considers animal species of different size, regular and predictable changes are seen in the relative proportions of the organs and the relative rates of physiological processes such as the metabolism and growth (Damuth, 2001). These scaling relationships are called allometries and have many ecological and adaptive implications (Kleiber, 1975; Schmidt-Nielsen, 1984; Peters, 1983). The following allometric expressing the scaling of some physiological or morphological parameter, y in accordance with changes in body size, M is well known:

$$y = aM^b. \tag{21}$$

The constants a and b are the same for "metabolically similar animals".

The search for similarities in the metabolic organization and growth of animals received much attention, one of the directions is looking for different invariants. Brown and West (2000) discussed diverse questions and aspects of scaling in animals and plants. Charnov et al. (2001) reported that a prominent feature of comparative life histories in fish and other indeterminate growers is the approximate invariance across species of dimensionless numbers made up from reproductive and timing variables. The two best known are age at maturity divided by average adult lifespan, and the proportion of body mass given to reproduction per year multiplied by the average adult lifespan.

Invariants have been empirically observed in animals also on the population level: species differing in body mass, M, by many orders of magnitude tend to have almost equal rates of energy use per unit area by the population, because of an inverse allometric scaling relationship between energy use by the individual, or its metabolic rate, B, and the maximal population density, N_{max}. Because $B \propto M^{3/4}$ and $N_{max} \propto M^{-3/4}$, energy use is proportional to $BN_{max} \propto M^{3/4}M^{-3/4} \propto M^0$. This phenomenon was defined by Damuth (1981) as "energy equivalence". Enquist et al. (1998) showed that this also holds for plants, namely that the allometric scaling of both B and N_{max} appears to be the same as in animals.

Growth rates, or rates of production of new biomass, are of fundamental importance in linking physiological processes to adaptively important features, such as reproductive rates and other life history variables. Among animal species, the rates of biomass production and growth are proportional to the metabolic rate, which scales as the 3/4 power of body mass (Kleiber, 1975; Peters, 1983).

The relationship between the mammalian basal metabolic rate, B, and body mass, M, has been the subject of regular investigation for over a century. Typically, the relationship is expressed as an allometric equation of the form (21). The geometric considerations relating volume to surface sizes predict $b = 2/3$. Some researchers show that in large-scale interspecific comparison, the basal metabolic rate and body size are related by an allometric equation with the value of exponent b approximating $3/4$ (Hemmingsen, 1960; Kleiber, 1975). The power $3/4$ in the scaling relationship is unusual from the point of view of geometrical considerations, though it proved to be valid for animals and plants in a range of studies (Schmidt-Nielsen, 1984; McMahon and Bonner, 1983; Brown, 1995; West et al., 1997; Damuth, 2001). West et al. (1997) argued that allometric scaling relations, including the 3/4 power law for metabolic rates, are characteristic of all organisms and derive them from a general model of transport of essential materials through space-filling fractal networks of branching tubes. Banavar et al. (1999) proposed a similar explanation based on branching transportation networks within the organism. In their subsequent work West et al. (1999) proposed to consider four-dimensional biology and suggested that the quarter-power scaling laws originate from hierarchical branching nutrient supply networks that terminate in size-invariant units, such as capillaries, leaves,

mitochondria, and oxidase molecules. They hypothesize that natural selection tends to maximize both metabolic capacity, by maximizing the scaling of exchange surface areas, and internal efficiency, by minimizing the scaling of transport distances and times. These design principles are independent of detailed dynamics and explicit models and should apply to virtually all organisms. Other researchers doubt the applicability of the "3/4 rule" of energy–size relationship. Dodds and Rothman (2001) considered value 2/3 obtained from simple dimensional relationships to be a null hypothesis testable by empirical studies. They re-analyzed several data sets for mammals and birds and found little evidence for rejecting $b = 2/3$ in favor of $b = 3/4$. The authors argued that present theories for $b = 3/4$ require assumptions that render them unconvincing for rejecting the null hypothesis that $b = 2/3$. The value of the scaling exponent, b, is a point of active debate in the literature, with sound arguments for and against geometric ($b = 2/3$) and quarter-power ($b = 3/4$) scaling.

4.2 Animal-plant unification

Plants exhibit degrees of modular construction, indeterminate growth, and form varieties that are greater than those shown by animals. However, until recently, the scaling of basic processes such as the metabolism and growth had remained undocumented for a representative sample of plant species. A book by Niklas (1994) on plant allometry is an early attempt to provide a unified treatment of plant form and function from an allometric perspective. Niklas (1994); Niklas and Enquist (2001) discussed allometry in plants and presented empirical allometric scaling relationships for rates of annual plant biomass production ("growth"), different measures of body size (dry weight and length) and photosynthetic biomass (or pigment concentration) per plant (or cell) in species ranging from unicellular algae to large trees. Annualized rates of growth G scale as the $3/4$ power of body mass M over 20 orders of magnitude of M (i.e. $G \propto M^{3/4}$); plant body length L scales, on average, as the $1/4$ power of M over 22 orders of magnitude of M; and photosynthetic biomass M_p scales as the 3/4 power of nonphotosynthetic biomass M_n. These scaling relationships are indifferent to phylogenetic affiliation and habitat and have far-reaching ecological and evolutionary implications. Rates of resource use in individual plants scale as approximately the $3/4$ power of body mass (Enquist et al., 1998). This is similar to the scaling of the metabolic rates of animals (Schmidt-Nielsen, 1984; McMahon and Bonner, 1983; Brown, 1995) and is predicted from a model of resource use in fractal-like branching structures (West et al., 1997). The mechanistic model of relationships between density and mass in resource-limited plants (Enquist et al., 1998) predicts that average plant size scales as the $-4/3$ power of maximum population density, in agreement with empirical evidence and comparable relationships in animals, but significantly less than the $-3/2$ power predicted by geometric models.

These new analyses reveal that growth scales among plants in the same way as it does among animals, and support the growing realization that the same scaling rules may apply to both animals and plants for similar reasons (Damuth, 2001). Many attempts have been made to consider scaling rules in plants and animals and to create a unifying approach, explaining the similarities between the structural and metabolic organization. Damuth (2001, 1998) reviewed advances in the comparative growth allometry of plants and animals and research towards unifying common laws of scaling and discussed general models that can be applied (with different assumptions) to both animals and plants noting among them the work of Banavar et al. (1999) on transportation networks and the theory of dynamic energy budgets (Kooijman, 2000). He reviewed the study of Niklas and Enquist (2001) on plant allometry and compared the results obtained on plants (trees) with those for "warm-blooded" (endothermic) and "cold-blooded" (ectothermic) metabolic animals. He compared the rates of growth of animals and plants over the size ranges that they have in common (Figure 11). The realized somatic growth rates of both plants and animals of comparable body mass are remarkably similar. This suggests that the cells of both plants and animals are similarly limited in the rates by which they can effectuate growth, just as the abilities of different-sized plants and animals to deliver energy to their cells are similarly constrained by scaling relationships. Banavar et al. (2002) proposed a set of scaling relations for age, mass, and other physiological traits that allow to display ontogenetic changes in different organisms (showing determinate growth) on a universal growth curve with dimensionless time and a mass ratio.

West et al. (2002) described the allometric scaling of the metabolic rate on a large scale, from molecules and mitochondria to cells and mammals. They performed a new analysis of the allometry of mammalian basal metabolic rate that accounts for variation associated with body temperature, digestive state, and phylogeny using data encompassing five orders of magnitude variation in M and featuring 619 species from 19 orders. The authors found no support for a metabolic scaling exponent of $3/4$. Their results demonstrate that $B \propto M^{2/3}$ (White and Seymour, 2003).

4.3 Growth and conservation laws

A valid theory of ontogenetic growth obviously should be consistent with the basic laws of conservation of mass and energy. Lika and Kooijman (2003) discussed the aspects of energy allocation in indeterminate and determinate growth strategies. Makarieva et al. (2004) analyzed the assumptions underlying ontogenetic growth models of West et al. (2001) and Gillooly et al. (2002) and argued that the basic relations in which these models are grounded contradict the law of energy conservation. They demonstrated the failure of these models to predict and explain several important lines of empirical evidence, including (a) the organismal energy budget during embryonic development; (b) the human

Figure 11: Comparison of growth rates of trees and vertebrates, plotted on a common scale. Polygons represent the regions occupied by the data points. The black unfilled polygon encloses tree data from (Niklas and Enquist, 2001). The endothermic vertebrates – mammals (large polygon) and birds (small polygon) – are in red, ectothermic vertebrates in yellow. Ectotherms and endotherms overlap in a narrow region. The regression line is that presented in (Niklas and Enquist, 2001). Vertebrate data recalculated from (Ricklefs, 1968) and (Case, 1978). (Reproduced from (Damuth, 2001)).
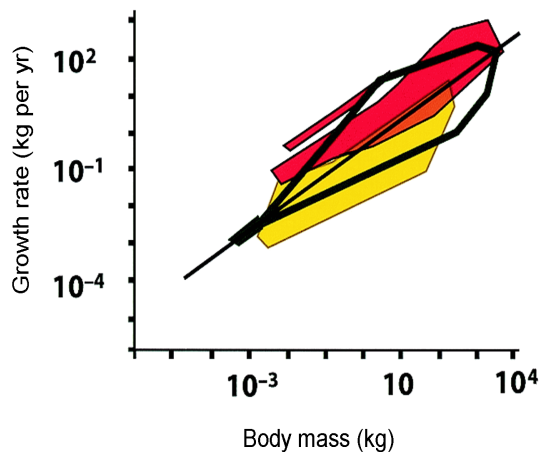
growth curve; (c) patterns of metabolic rate change during transition from embryonic to post-embryonic stages; and (d) differences between the parameters of embryonic growth in different taxa. They also show how a theoretical approach based on well-established ecological regularities explains observations where the formal models fail. Within a broader context, the authors discussed the major principles of ontogenetic growth modeling studies in ecology, emphasizing the necessity of ecological theory to be based on assumptions that are testable and formulated in terms of variables and parameters that are measurable.

5 What shapes the trajectories of growth?

Size is an important life history variable closely relating reproduction to survival. Size impacts survival via influencing physical strength, the ability to evade predation, to with-

stand environmental hazards and to obtain food. Size influences reproduction via success in mating, fertility, and the survival of the offspring due to size-specific differences in feeding and care. Mate competition is an important reason to grow for fish, elephants, deer, kangaroos, water mammals, and many other species often favoring indeterminate growth. In many species (e.g. fish), size affects reproduction and survival and hence, individual fitness more than age (e.g. see the discussion on the dependence of survival, flowering, and fertility on size in perennial plants in (Metcalf et al., 2003))

A larger size usually means better survival and reproduction, but growth has its costs. The maintenance of the body requires energy, which is increasing with the body mass, growth requires additional energy and resources. Energy and resource requirements of growth and maintenance compete with those of survival (mobility, immune defence) and reproduction. For this reason, growth is tightly linked with strategies of resource allocation.

Growth strategies have been molded by resource allocation and other factors during evolution, a process which is assumed to increase fitness. It is important to understand what fitness is. Several theoretical measures of fitness have been developed and used in literature, such as expected lifetime fertility, R_0, the intrinsic rate of increase, r, invasion fitness (a population dynamics version of Maynard Smith and Price (1973) evolutionary stable strategy (ESS) concept (Metz et al., 1992; Rand et al., 1994; Ferrière and Gatto, 1995)). There is no generally agreed-on measure of fitness, and the application of different measures often leads to controversial results. It has long been puzzling to ecologists and geneticists which of these fitness measures, if any, should be regarded as the correct one (Heino and Kaitala, 1999; Kozłowski, 1993; Pásztor et al., 1996). Mylius and Diekmann (1995) and Metz et al. (1996) clarified the subject and showed that the fitness maximization approach may coincide with the invasion fitness concept only if population size is stable and if environmental feedback is one-dimensional, i.e. there is only one density-dependent factor influencing the population. Selecting a certain fitness measure means assuming implicitly a certain way in which density dependence affects the individuals in the population under study – a fact that is often overlooked. Such implicit assumptions may strongly constrain the result of the studies and render it incompatible with the original problem.

Recent decades brought an exploding number of theoretical and experimental works in which optimal allocation strategies and their outcomes have been studied (see (Kozłowski, 1992) for a review). Usually, organisms with determinate growth are considered, and works such as these are abundant. Works on allocation considering indeterminate growth, however, are few. Charnov et al. (2001) addresses the conditions under which the evolution of life histories can lead to the development of indeterminate growth patterns in fish and lizards. Heino and Kaitala (1999) reviewed resource allocation between growth and reproduction in animals with indeterminate growth.

The first models of allocation between growth and reproduction focused on annual plants. In these models, the determinate growth patterns always turned out to be evolutionary optimal. Heino and Kaitala (1999) reviewed the problems of obtaining indeterminate growth patterns as solutions of the models of optimum allocation and discussed the effects of the environment on the development of resource allocation schemes. Among the factors that could favor the development of indeterminate growth patterns, they noted:

1. Ecological factors (varying length of the growing season in annuals that may select for graded change from the allocation to growth to allocations to reproduction (Cohen, 1971, 1976), seasonality as such in perennial species). In perennial plant species, an optimal allocation pattern resulting in indeterminate growth may include a number of seasons during which early season is devoted only to growth, and late season only to reproduction (Kozłowski and Uchmañski, 1987). If reproduction occurs before growth, this favors determinate growth. The loss of somatic tissues in plants between the seasons may influence the possibility of indeterminate growth patterns (Pugliese and Kozłowski, 1990).

2. Physiological factors (trade-offs and constraints limiting reproductive effort), or

3. A combination of both of these factors (size-dependent mortality and production rates both increasing or decreasing, diminishing marginal returns from reproductive investment). For instance, indeterminate growth was found to be optimal when both production and mortality rates increased with body size in simulations of a *Daphnia* (Taylor and Gabriel, 1992). Perrin et al. (1993) (see also (Perrin and Sibly, 1993)) proved the result analytically; an adult growth rate can also occur if both production and mortality decrease with size. Both of these situations may apply in nature.

Brown et al. (1993) developed a general model for the effect of body size on fitness defining fitness as reproductive power, the rate of conversion of energy into offspring and thus proposed an energetic definition of fitness that may help to unify models of ecology and evolutionary biology providing a common "currency". This energy definition of fitness was discussed and criticized by (Kozłowski, 1996). Heino and Kaitala (1999) looked at indeterminate growth as a special kind of bet-hedging strategy.

Physiological limitations

Growth is constrained by physiological limitations such as physical strength which is limiting mass in large animals such as elephants (Laws, 1966), height in trees (Koch et al., 2004), even the growth of small plants, such as tomatoes and beans, and by structural constraints such as limiting growth of reproductive organs. The water supply is a factor limiting leaf structure and density, photosynthesis capability and carbon dioxide concen-

tration in very high trees, such as redwoods. Koch et al. (2004) showed that the tallest a tree could grow would be about 130 m according to these limitations.

Growth can also be risky in itself. In certain animals (such as crabs), having a rigid outer shell growth is related to moulting – the periodical shedding of an old shell and the growing of a larger one. The process of shedding has several precisely timed steps, failure leads to the death of the animal. Moreover, the possibility of predation increases during the moulting process.

Ecological limitations

Annual organisms grow, mature, and reproduce in one season. They cannot survive the seasons unfavorable to them as adults and reproduce again, and this favors determinate growth as an optimal pattern. Perennial animals and plants may grow after reaching sexual maturity, and have patterns synchronized to seasonal changes (e.g. have a period of growth at the beginning of the season and reproduction at the end). Parts of plants may have different growth patterns. The trunk (main body) grows indeterminately, but leaves and reproductive parts, such as flowers and fruit, have a determinate final size. Leaves grow in the beginning of the season, they provide photosynthesis and gas exchange. They wear and tear quickly, and have no chance of surviving the unfavorable season. Keeping them may be risky for the main body, so in the end of the season the nutrients are removed from the leaves and they are shed. The cycle is repeated the next season. Optimal strategies of growth and reproduction in variable environments were studied in plants by Amir and Cohen (1990). de Lara (2003) presented a general mathematical model of resource allocation and proved that determinate growth is the optimal strategy in a deterministic environment, whereas a stochastic environment gives rise to optimal strategies with indeterminate growth.

Models that define fitness in terms of the per capita rate of increase of phenotypes are used to analyze patterns of individual growth. Sibly et al. (1985) showed that sigmoid growth curves are an optimal strategy (i.e. maximize fitness) under the following assumptions: mortality decreases with body size; mortality is a convex function of a specific growth rate, viewed from above; there is a constraint on the growth rate, which is attained in the first phase of growth. If the constraint is not attained, then the size should increase at a progressively reducing rate. These predictions are biologically plausible. Catch-up growth, for retarded individuals, is generally not an optimal strategy though in special cases (e.g. seasonal breeding) it might be.

Growth may be advantageous after first breeding if the birth rate is a convex function of G (the fraction of production devoted to growth) viewed from above, or if the mortality rate is a convex function of G, viewed from above. If these assumptions both are false, growth should cease at the age of first reproduction. These predictions may be used to evaluate the incidence of indeterminate versus determinate growth in the animal kingdom.

Katsukawa et al. (2002) noted that many mammals and birds have determinate growth, whereas the organisms in a number of other taxa have indeterminate growth. The authors discuss the conditions under which each of the following strategies are optimal: semelparity, iteroparity with determinate growth, and iteroparity with indeterminate growth. They propose a stage-structured model to describe optimal energy allocation among growth, reproduction, and survival. The model demonstrates that iteroparity with indeterminate growth is selected for when a nonlinear relationship exists between weight and energy production; this strategy is also often selected for in stochastic environments, even with a linear relationship between weight and energy production. The optimal strategy in the stochastic environments is to maximize the long-term population growth rate, which does not correspond with the maximization of total fertility. Optimal life history is determined by a balance between spreading a risk and increasing the number of offspring. The model suggests that the optimal life history strategy depends on the magnitude of environmental fluctuations, the advantage of investing in growth, the cost of survival, and the nonlinearity between weight and energy production.

Von Bertalanffy's equation (see 3.3.1) is commonly used to model indeterminate growth (Czarnołeśki and Kozłowski, 1998). Von Bertalanffy claimed that this growth pattern results from growth potentially decreasing with age. An alternative approach provided by life history theory predicts that indeterminate growth is optimal for organisms in a seasonal environment and results not from a decreasing growth potential but from allocating increasingly less energy with age to growth and more to reproduction. Von Bertalanffy's curves are the result of evolutionary optimization. They should not be used in optimization models as an assumption but rather as a tool to describe the indeterminate growth pattern phenomenologically.

Heino and Kaitala (1999) reviewed theoretical developments explaining the evolution of age-schedules of reproduction in animals with indeterminate growth. They also compare studies on animals and plants with indeterminate growth when they can be interpreted in common terms. The authors discussed different measures used to determine the fittest life histories, indeterminate growth as a problem of resource allocation, and the effects of the environment on the development of resource allocation schemes.

Despite of these efforts, the theories on resource allocation between growth and reproduction remain almost completely untested (Heino and Kaitala, 1999). An anecdotal, but provocative idea on the evolution of a specific growth strategy may be the following. Animals generally grow determinately because they usually can move through environments. Plants frequently show indeterminate growth – they cannot move and hence they grow through the environment; indeterminate growth allows plants to increase exposure to air, sunlight, and soil throughout their life.

6 Problems and prospects

The commonly used definitions of determinate and indeterminate growth patterns (given in the introduction) may lead to confusion. Differences between growth strategies may be understood in terms of size – whether or not an animal has a predefined maximum size, or in terms of age or stage – whether an age, or stage at which growth stops, such as the age of maturity, exists or not.

Indeterminate growth does not mean that an organism can reach any large size if it survives long enough. Nothing can grow without limit because of structural and resource limitations and all organisms, if they survive long enough, will reach their maximum size determined by physiological constraints. In the wild, they may die well before reaching the asymptotic size and growth may seem unlimited. The main difference between determinate and indeterminate growth is that the first stops at some point in life, usually at, or soon after, reaching sexual maturity, and the second does not stop as long as the organism survives.

The existing definition of determinate and indeterminate growth patterns is based on age: growth is determinate if the organism reaches its maximum size at some age (usually around sexual maturity) and indeterminate if the growth continues at any age. Life histories have been shaped by an evolutionary process that increases the fitness of species. Fitness is dependent on life-history variables, such as the age of sexual maturity, and age-specific fertility and mortality; these variables are not less important than age. The definition of indeterminate and determinate growth patterns should be revised, because of problems with interpreting experimental data. The traditional definition of determinate and indeterminate growth patterns may not be sufficient for studies on life-history evolution and alternative definitions should be considered. It may be useful to consider other alternative definitions of growth patterns based on variables other than age, such as:

Definition based on survival: growth is determinate if an organism reaches maximum (asymptotic) size when many individuals of the population are still alive, and indeterminate, when very few individuals are alive. This kind of growth may continue long past the age of sexual maturity.

Definition based on reproductive value: growth is determinate if an organism reaches maximum (asymptotic) size when most reproduction is yet to occur, and indeterminate when most reproduction has already occurred.

Detailed studies of growth strategies are desirable to assess the fundamental biology of growth, resource allocation, aging, and longevity in higher organisms. This may help to verify the "universality" of determinate growth in mammals or whether the determinate growth stops at, or soon after, the age of maturity in all species.

7   Acknowledgements

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