A Mathematical Model of Skeletal Development
(as exemplified in equine height increases)[*]

Interest in the development of horses resulted in the accumulation of a large amount of growth data on various measures at various stages of development. Not all of these exhibited an invariance that was a useful predictor of characteristics that would be realized in the mature individual. Height at the withers does, however, show such invariance, and the equations that describe its development suggest a model of development of the associated bone structures.

I. Introduction

From direct measurements of the horses foaled on our farm over a period of many years it became evident that height increases associated with the development of the column of bones in the forelimb of the horses (as shown in figure 1) follow an invariant pattern under normal conditions. This invariant pattern is accurately represented by two mathematical equations applicable to two distinct phases of development. The first is a linear growth phase persisting for a couple of months after birth. The equation for height growth during this phase is:

$$1) \qquad h(t) = 0.089 \, h_B \, t$$

where h(t) represents height in inches as a function of time, t, measured in *standard months* (30.5 days) since conception, and the parameter h_B is the height at foaling.

The second and final phase of skeletal development is characterized by a monotonically decreasing growth rate from about 3 months of age until maturity. Precise agreement with the growth data is obtained using the exponential distribution function:

$$2) \qquad h(t) = h_M \left(1 - e^{-0.1086 \, t} \right)$$

In this equation h(t) and t are as defined above and h_M is the height at maturity; e is the base of the natural logarithm (approximately 2.7183).
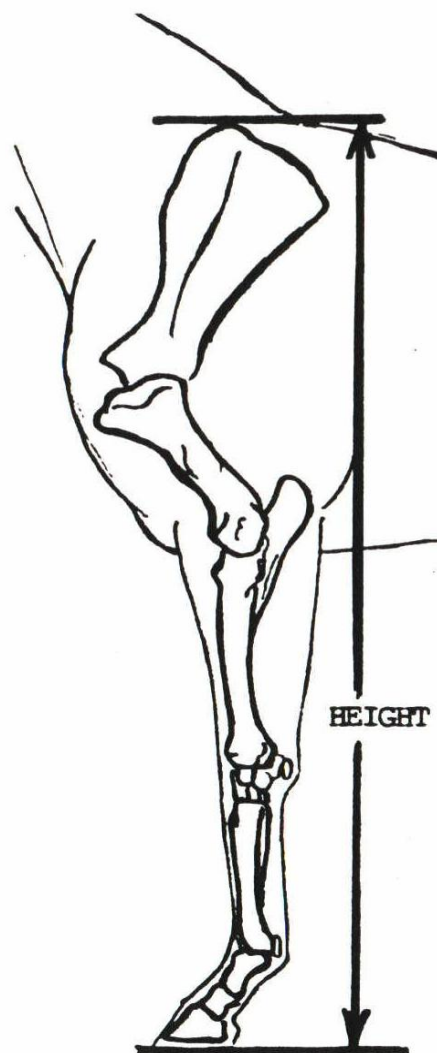

Figure 1: "Height" as measured at the withers

The constants in both equations are determined to obtain a best fit to the actual growth data. The two equations are plotted in figure 2. The plus symbols represent actual height growth data for an individual that was 40.5 inches in height at foaling and matured to a height of 16 hands (64 inches).
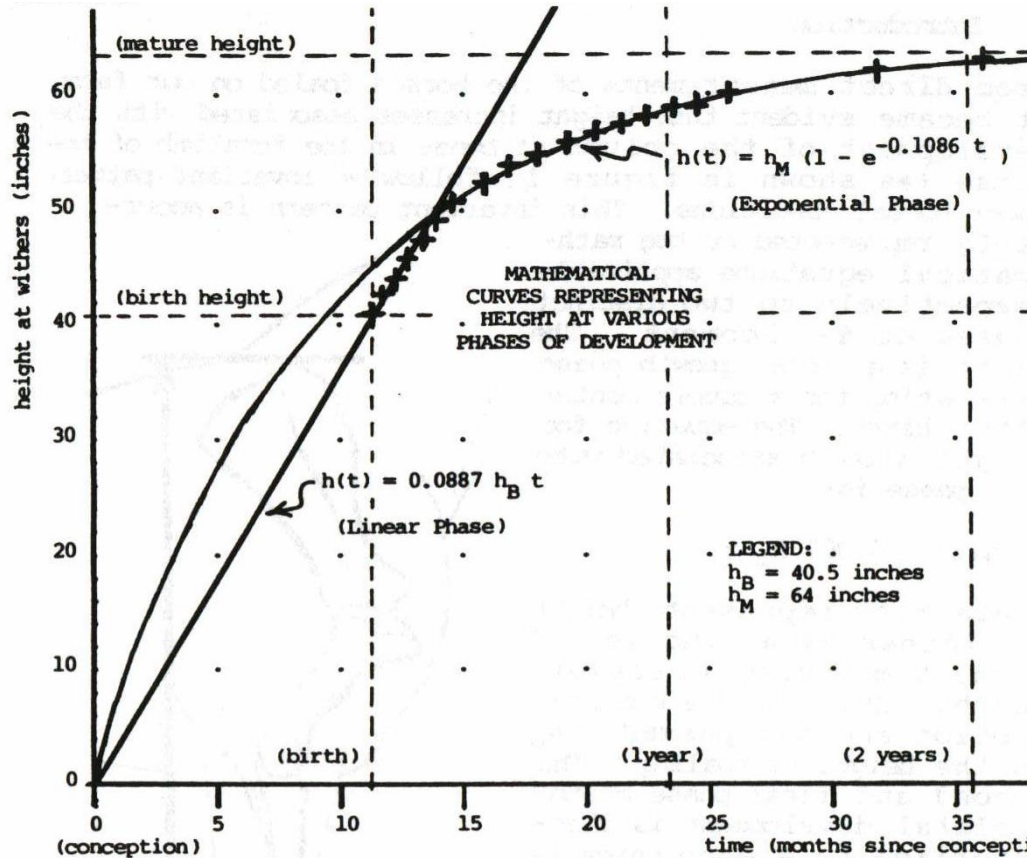

Figure 2: Equine Height Growth Pattern

The fact that these two empirical equations so accurately describe the associated growth data beginning at foaling and persisting through the first months in the first case, and from that point through maturity in the other, and yet both converge at zero height at 344 days prior to foaling (coinciding with the most typical duration of pregnancy), suggests that the equations are in some sense essential to the description, and derivative from the actual processes involved in equine skeletal development!

To check whether this were indeed a possibility, "heights" were estimated for eleven fetuses aborted between 2 and 11 months after conception. This data corroborates nearly linear increases in this "height" parameter characterizing prenatal developments as shown in figure 3.

The simplicity and regularity of these height growth patterns suggest the possibility of discovering a correspondingly straight-forward model of the underlying growth mechanisms. Models of physical processes often provide the capability of predicting phenomena that, although not previously noticed, can thereafter be observed and studied. If certain patterns are to be avoided or encouraged, such models provide strategic tools for developing methods which avoid or encourage their occurrence. In addition, a skeletal growth model would have considerable didactic value in promoting an understanding of the associated growth mechanism.
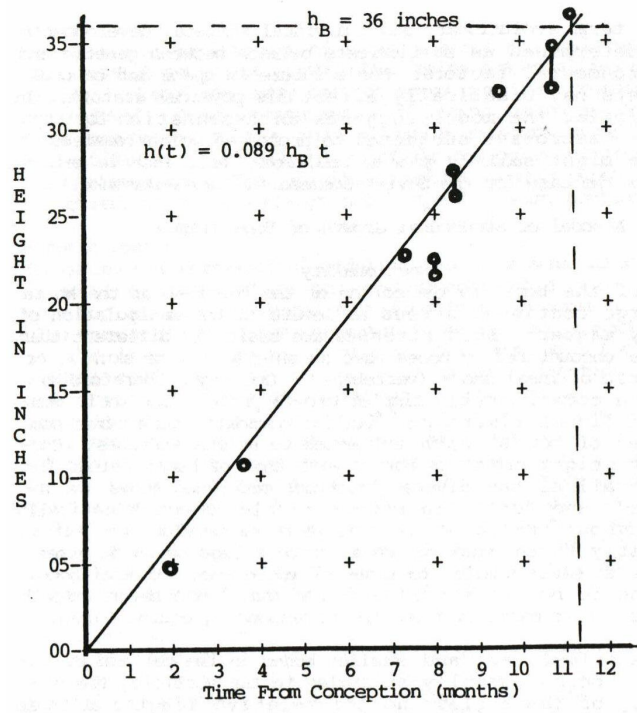
Figure 3: Prenatal development of "height" structures

A general model of skeletal development is constructed in this paper from which equations 1 and 2 can be derived. Three unique types of anomalous growth phenomena are predicted by this model for which examples have been observed.

The model is extensible to skeletal developments of human beings and other species. The model suggests that both the long term evolutionary and individual developments are determined as an intricate balance between genetic and environmental factors. Man's future in space and on other planets may drastically affect his physical stature. In particular, the model suggests an explanation for why a mature astronaut subjected to prolonged weightlessness in space might suddenly grow an additional half inch in height as has repeatedly been documented although the rationale that has been disseminated suggests a predisposition to accept other factors. The soviet astronaut Yuri Romanenkol was the first reported incidence of this phenomenon.

II.   A Model of Structural Growth of Bone Tissue

Functionality

All of the bones in the column of the forelimb of the horse undergo continual stress as levers in the manipulation of heavy weight. Such stresses are basically different than those encountered by bones used as shielding (the skull), or to absorb lineal shock (vertebrae). One might therefore expect a commensurably simpler growth pattern for their combined lineal dimension than for composite structures comprised of bones subjected to unique stresses. Contrast height growth in horses to that of human beings for which all of the diverse functions mentioned above are involved, and for which stress levels change dramatically throughout the first several years of development. It is probably three years before a person's legs begin to experience stresses similar to those of

adolescence and adulthood. It should therefore not be surprising that human height growth curves differ markedly from the corresponding equine curves.

The shoulder, arm, and smaller bones in the pastern of the horse, being normally at angles to the vertical, the constancy of the angles and the relative lengths of these individual bones with age is required in order that they contribute a continually proportionate amount of the overall height of the structure. Since this condition is met to a large degree, the rate of increase of equine height can be seen to be proportional to the rate of increase in the lengths of the individual bones in the forelimb. It is evident that in horses, height provides a measure of length of bone tissue continually being stressed as levers. These two measures are therefore treated interchangeably throughout the remainder of this paper. The model will address bone growth and function; measurement will involve equine height.

Biological Processes

The ability to convert environmental nutrition to support the reproduction and development of an organism according to type is fundamental in living systems. So also is the ability to maintain the developing organism against the routine and extraordinary hazards of its environment.

These basic requirements of living systems are allocated unilaterally to constituent cells rather than being a specialized capability of some. Each and every cell of every organ and organism is so endowed. Growth measurements of living tissue are therefore measures of multiplication rates of the cells and the efficiency of allocation of the new cells within emergent structures. The individual factors in this paradigm of structural growth are elaborated in the following sections:

Mitotic Factor

To obtain a mathematical model of growth of bone structure, we will define "c" as the maximum achievable rate of conversion of environmental nutrition in the process of cellular production. The parameter is seen to be proportional to the inherent rate of mitosis associated with individual cells in the system. It is not a function of the collective system such as how many cells comprise it or how long it is. It is rather a function of the abundance of nourishment in the environment and the conversion efficiency of its individual cells. To simplify our model initially, it is assumed that there is a plethora of environmental nourishment such that c is limited solely by inherent metabolic efficiency. Since each cell reproduces in kind, we can assume that the cells in each generation are characterized by the same conversion efficiency. Thus c will be a constant for a given individual, independent of time.

Developmental Factor

As cells are produced, they are allocated within emergent structure in an orderly fashion so as to maintain the genetically determined structural organization. The parameter "g" is defined as the proportion of this allocation process along the direction of measured growth. It can be viewed as the proportion of the produced cells to be used in creating new structure beyond its previous extent and coincident with the direction of interest. This chosen direction in our current investigation is along the length of the growing bones. This direction happens to agree with the primary thrust of the allocation process for bones, which at least in post-natal developments, involves emanation at the epiphyses with continuous ossification into the structure of the bone. Therefore g is the production function for height; it is proportional to the rate of lineal increase in the length of the bone:

3) $g = \alpha\ dh(t)/dt$

where α is an effectiveness coefficient whose value is to be determined, and $dh(t)/dt$ is the time derivative of height (how rapidly it increases with time).

In early embryonic stages of development this characterization is much less accurate, and in fact a much larger percentage of bone development is applied to the development of bone thickness. In our model we will denominate such developments associated with new structure that is not in the direction affecting what we measure as "height" with the symbol "f". "Height" increases will not exhibit a direct dependence on any such factors, but they will diminish the effectiveness of c with regard to our parameter of interest.

Environmental Damage Factor

A certain proportion of the new cells must be allocated to repairing damaged structure if the organism is to survive. To maintain viable structural functionality this repair rate "r" must be greater than or equal to the rate of destruction of cells experienced by the structure, in this case of the bones in the foreleg of the horse. The environment for these bones involves continual stress associated with use as levers, for which mechanical forces which tend to break them (in destroying the individual cells in the bone) are proportional to their lengths (height in measurements). Of course the rate of the destruction is also dependent on the frequency and specific amount of the force with which the lever is used, but to simplify the model we assume that the accumulated effects of mechanical stress over time intervals significant to cellular production remain approximately constant within each phase of development. The amount of cellular production required to effect repairs can therefore be expressed as follows:

4) $r = \beta\ h(t)$

where β is the coefficient relating stress to damage rate, i. e., the value of β determined by the stress level and the inherent structural integrity of the allocated cells. (It would take on a different value on the moon than on earth.) Its value is to be determined.

Illustration of the modeled Process

To understand the development of cellular structure from individual cell divisions as it has been modeled above, refer to figure 4. The figure illustrates the contribution of the cells in their various stages of mitosis to the overall structure. The sketch is of a microscopic view of a thin slice of tissue, with chromosomes and membranes of the individual cells emphasized. Parameter c is proportional to the number of cells which subdivide in an interval of time. The directionality of the subdivision process within the structure together with its orientation relative to the direction being measured will determine the value of α. The factor β will be proportional to the number of cells destroyed in an interval of time.

Basic Equations of the Model

Since mitotic conversion and environmental nutrition supports both the genetically determined direction of growth and the maintenance aspect of structural development, the fundamental equation of the model can be written as:
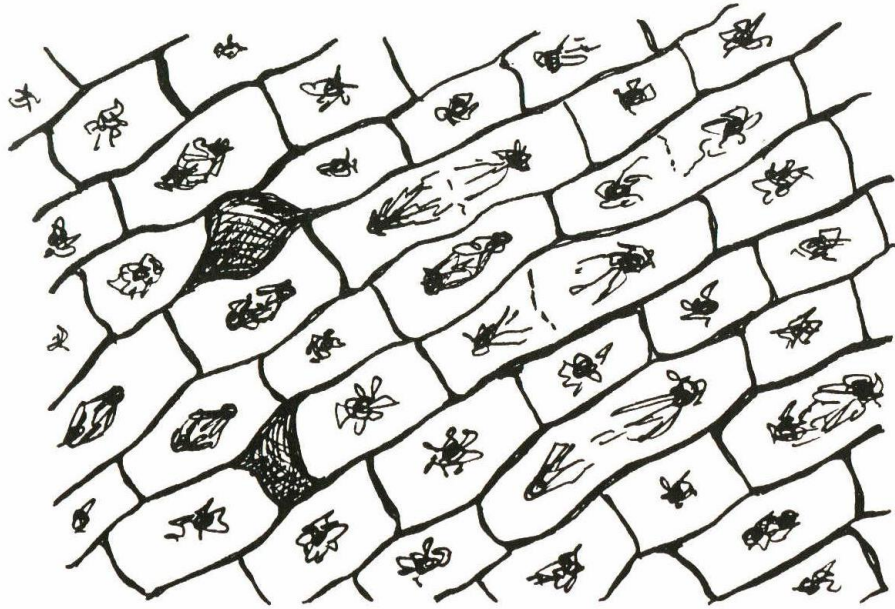
Figure 4: Illustration of structure comprised of cells

5) $c = f + g + r$

By substitution of equation 3 and 4 into equation 5, we obtain a fundamental differential equation for h(t) as follows:

6) $dh(t)/dt + \beta\, h(t) = A$, where $B = \beta / \alpha$ and $A = (c - f) / \alpha$.

Equation 5 applies to all cellular structural developments in organisms and organs. Equation 6 is restricted to skeletal developments, and specifically skeletal components (bones) subjected unilaterally to continual stresses as levers. It will be specific to equine height when specific values have been determined for A and B appropriate to horses by fitting the resultant curves to data like that shown in figures 2 and 3 above.

   Height at the rump of the horse follows the same pattern as height at the withers even though the bones have different relative lengths and corresponding angles to the vertical. The similarity in growth pattern derives from the basic similarity of function. Length from chest to buttocks on the other hand employs different functionality and is therefore characterized by its own unique growth pattern. Hence a horse's length-to-height ratio does not remain constant as he matures. In addition to parametric differences between functional bone groups, separate phases of development may impose different stresses on the bones, which therefore induce unique values of B even for the same functional bone group.

   We now have a basis for understanding structural groupings of bones and phases of development based upon similarities of stresses for which parameter values may be assumed to be unilateral for all members of the group, and constant for the duration of the phase of development. These definitions of functional groups and development phase are intricately related to the mechanism of growth. In human development there are more phases involved, for example: Prenatal, infancy, crawling, walking, and later the more rigorous athletic stresses. Furthermore, height in humans is not comprised of bones in a single bone group as discussed earlier.

In horses there are basically only two phases: Prenatal and athletic stress. In the first phase the environment is buoyant and therefore β (implying B) is approximately zero, but bone development is not strictly lineal as in postnatal developments, so that we might expect different values for the parameter, f (and therefore A) in the two phases. Thus in the prenatal phase, we would expect bone development characterized by a unique value of $A_1 = (c - f_1) / \alpha_1$ and $B_1=0$. (Numeric subscripts refer to phase.) The solution of equation 6 in this case is just equation 1 if we assign the value $A_1 = 0.089 \, h_B$.

For the postnatal development phase we would expect a characterization of, $A_2 = (c - f_2) / \alpha_2$ and $B_2 = \beta / \alpha_2$. The solution to equation 6 in this case is the exponential distribution function given earlier as equation 2, if we make the assignments, $B_2 = 0.1086$ and $A_2 = 0.1086 \, h_M$.

III.   Characteristics of the Skeletal Growth Model

Thus it has been shown that the simple model of skeletal development accounts for normally observed equine skeletal height growth patterns. In particular it provides a derivation for the mathematical equations which accurately represent the equine height growth data shown in figure 2. There are, however, certain aspects of the model that need further explanation. These features may reveal extremely interesting facets of skeletal growth phenomena.

Phase Transitions
Equine skeletal growth as it has been modeled is characterized by two distinct phases of development: pre- and post-natal. And yet we see that the initial growth pattern continues until two or three months after foaling! This may be explained as follows:
When the foal is born and begins using its legs to walk and then almost immediately to run and hop around, the cells in these bones begin to be destroyed at a rate proportional to the foal's height. But initially the legs are "brand new" with no damaged cells that defines the equilibrium for which the phase 2 equation applies. So with no incumbent damage to be repaired, growth proceeds linearly as though nothing has happened. Gradually more and more damage occurs and a little larger percentage of the cell production must go into repairing structure rather than just adding to existing structure. It is not until several months after foaling that the requirements for repair mount up to the percentage that will define the new equilibrium condition described by equation 2. Consider a cross section of the bone similar to what is shown in figure 4: Normally there will be a certain percentage of the cells in the cross section in need of repair to maintain the integrity of the structure. For a given height and stress level this percentage would be constant, but at birth it is nearly zero and only gradually approaches the accumulated damage as it reaches the new growth profile appropriate to the equilibrium values for which the number of cells being damaged and repaired are equal. The foal being born smaller than the postnatal profile results in a lower damage rate (while accumulated damage is still small) and height will not "overshoot" a safe height for the individual while the transition takes place smoothly over a longer period of time.

Parameter Value Changes with Phase
That B=0 in the early embryonic and fetal stages of development and is appreciable after the foal is born is fully accounted by the model since gravitational forces are all but totally nullified in the buoyant environment of the uterus. B is a physical characteristic of the environment which changes dramatically between these two phases.

On the other hand, the change which occurs in f (and therefore in A) is an organizational change which would seem to take place almost as if it were only coincidentally at the time of birth as far as the model is concerned. It is not a *deus ex machina* of the model, however. The coincidence of this phaseover is extremely essential to the viability and therefore of survival of the equine species and can therefore be considered as being a necessarily induced evolutionary factor – which is to say, "It happens because if it didn't, there wouldn't be any horses."

If $A_1 = A_2$, a horse's height at birth could reach 1.9 times what could be supported as a mature height, which is to say that the protected environment of the uterus would support the development of a length of bone structure that mitosis could not maintain once it became employed as a lever. It would in fact necessitate early parturition to avoid the foal becoming larger than its dam at foaling. Such individuals would break their legs immediately upon leaping to their feet shortly after birth, die on that account and never reproduce as selfish genes require. But once the bones attain an appreciable damage percentage, the danger of lengthier bones disappears since only the cellular production in excess of that required for repairs seems to be applied to structure extensions. Evolutionary factors tend to favor larger individuals as indicated by the more or less continuous evolutionary height developments from eohippus to Secretariat, so the need for a large value of f is dramatically reduced.

Time-Independence of the Fundamental Growth Equation

The growth data represented by equation 1 and 2 indicate that height is a continuously increasing function of time and we therefore think of growth as a basically temporal phenomenon wherein growth rate is determined by age. However, the characteristic differential equation can be rearranged with coefficient substitutions as follows:

7) $dh/dt = 0.1086 \, (h_M - h)$

Here we see that the rate of change of height is *not* an explicit function of time at all. And therefore height is not implicitly a function of time either! That is to say that although height (and its rate of increase) changes *with* age, it is not *because* of age, and is therefore not determined *by* age! According to the characteristic equation the rate changes only as a function of the current height and the genetically determined mature height.

An interesting aspect of this is the prospect for under nourished individuals regaining an optimal growth profile subsequent to obtaining a proper diet. Such anomalous growth behavior has been observed by the author and his wife with horses that were too small for their age when they came to our farm at various stages and subsequently experienced sustained growth spurts that put them on a profile that was appropriate to individuals who were as much as six months younger. So as long as there is no severe damage from deprivation, "predetermined" mature heights h_M can be reached by slower growth profiles.

IV.   Summary and Conclusions

On a regimen of sufficient nutrition horses exhibit an invariant height growth pattern. This pattern is characterized by two distinct phases that can be represented by very basic mathematical formulas. These two formulas share a common point of origin which corresponds to the point in time at which the individual was conceived. This suggested to the author that there might be something very basic to the developmental process in the form of these equations. A simple model

of growth was constructed that took into account genetic, metabolic, functional, and environmental factors. The model was shown to match the data precisely and to predict anomalous phenomena that have been observed.

Several questions are left unanswered with regard to the mechanism of switching parameter values in the model between phases, and in particular between pre-and post-natal phases of development.

Understanding skeletal growth phases and functional bone groupings introduced by the model clarifies differences and similarities in human and equine height development. It seems to the author to account also for some portion of the growth spurts experienced by astronauts left in weightlessness for prolonged periods of time.

The author has also wondered how such massive dinosaurs could have functioned – particularly such long skinny-necked species for which Galileo's analyses of giants in which the weights of their bodies necessitate grossly different conformation in bone length to width ratios, etc. Such analyses should apply to the appearance of the large dinosaurs relative to smaller ones and the reptiles all of which exhibit very similar form. Since developing this model the author believes that the large dinosaurs were aquatic, habituating bodies of water with swampy fringes. But that is far afield.

the author and his horse

the author when
horses were a major
part of his life