GENETIC SIZE AND GROWTH

IN GOATS

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GENETIC SIZE AND GROWTH IN GOATS

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STELLINGEN

1. De schalingstheorie van Taylor (1985) draagt bij tot een beter begrip van de biologische basis van genotypische variatie doordat het een onderscheid maakt tussen variatie als gevolg van verschillen in ontwikkelingsstadium en genetische grootte, en overige diertypische variatie.

   Taylor, St C.S. 1985. Use of genetic size-scaling in evaluation of animal growth. Journal of Animal Science 61 suppl. 2: 118-143.

2. Meerfasige allometrische groeipatronen kunnen op basis van de hierin te onderscheiden fasenovergangen een indicatie van genetische grootte geven voordat volwassenheid is bereikt.

   Dit proefschrift.

3. Kennis van de relatie tussen genetische grootte en het allometrische transpositie verschijnsel (White and Gould, 1965) maakt het mogelijk de intercept parameter in het simpele allometrische model op de juiste wijze te interpreteren.

   White, J.F. and Gould, S.J. 1965. Interpretation of the coefficient in the allometric equation. The American Naturalist 99: 5-18.
   Dit proefschrift.

4. De mate van volwassenheid van een dier wordt beter gekarakteriseerd door de fractie van een genetische grootte-maat dan door metabolische leeftijd.

   Dit proefschrift.

5. Het door Blaxter *et al.* (1982) beschreven gewichtsverloop van *ad libitum* gevoerde schapen en de daarmee gepaard gaande ontwikkeling in lichaamssamenstelling, resulterend in vetpercentages van meer dan 55% van het digesta-vrije gewicht, toont de beperkte bruikbaarheid aan van 'volwassen' gewichtsniveaus van 'normale' landbouwhuisdieren als maat voor genetische grootte.

   Blaxter, K. L., Fowler, V. R. and Gill, J. C. 1982. A study of the growth of sheep to maturity. Journal of Agricultural Science, Cambridge 98: 405-420.

6. Theorieën op het gebied van voederopnameregulering schenken onvoldoende aandacht aan de effecten van de mate van volwassenheid op het opname-niveau.

7. Voorafgaand aan het streven naar volledige integratie van het internationale MSc-onderwijs in het reguliere onderwijs aan de Landbouwuniversiteit dient de vraag beantwoord te worden of volledig Engelstalig onderwijs in de doctoraalfase aanvaardbaar en wenselijk is voor Nederlandstalige studenten en docenten.

8. Het verdient aanbeveling nader te onderzoeken in hoeverre de essentie van artikel 450 van het wetboek van strafrecht, waarin het nalaten van hulp aan iemand in direct levensgevaar strafbaar wordt gesteld, internationaal van toepassing is op Europese regeringsleiders die de genocide in het voormalige Joegoslavië negeren.

9. De huidige strenge regulering van mestproduktie op het platteland staat in schril contrast tot de bestuurlijke tolerantie ten aanzien van die op de stedelijke trottoirs.

10. De dagelijkse vermelding in televisie-journaals van de gemiddelde koersontwikkeling van aandelen op de internationale beurzen heeft een zeer geringe nieuwswaarde voor het algemene publiek en kan beter achterwege gelaten worden.

11. Zowel de uitdrukking 'hardlopers zijn doodlopers' als de wat modernere variant 'hardlopers zijn dopinglopers' bevatten een kern van waarheid.

12. De gretigheid en snelheid waarmee geiten op papier vastgelegde experimentele gegevens weten te consumeren wijst op een bijzondere vorm van wetenschappelijke honger.

Stellingen van Nico Ogink behorende bij het proefschrift: 'Genetic size and growth in goats'.
Wageningen, 19 oktober 1993.

VOORWOORD

De totstandkoming van dit proefschrift kent tal van raakvlakken met het biologische groeiproces. Het uiteindelijke resultaat in gedrukte vorm kan niet anders dan een beperkte éénzijdige indruk van de omvang en aard van dit proces weergeven. Een aanvullende beschrijving van de inspanningen van de vele betrokken personen tijdens de opeenvolgende groeistadia is hier daarom op zijn plaats.

Gedurende de uitvoering van het onderzoek en de verwerking van de onderzoeksgegevens was er de continue steun van mijn promotor en copromotoren. Groeiprocessen verlopen zelden zo glad en voorspelbaar als theoretische groeicurves willen doen geloven, maar kennen vaak een veel grilliger en onzekerder verloop. Het voortdurende vertrouwen en geduld dat Prof. Dick Zwart gedurende dit proces in mij stelde was hierbij van essentieel belang, waarvoor mijn erkentelijkheid. Wiebe Koops was de drijvende kracht achter het ombuigen van fasen van stilstand tot vooruitgang, zijn steun en inbreng gedurende de analyse van de gegevens heb ik als onmisbaar gevoeld. De onderzoekservaring en kennis van Bert Tolkamp vormden eveneens een belangrijke stimulans tot vooruitgang. Wiebe en Bert bedankt.

Mijn dank gaat ook uit naar de mensen die gedurende uiteenlopende fasen hebben bijgedragen. Gerrit Zemmelink, de initiator van het proefplan en projectleider gedurende de eerste jaren, en P. Bergström van het IVO te Zeist waren deel van mijn begeleidingsteam tijdens de eerste experimentele fase. Anne Waanders verleende met veel inzet en betrokkenheid de technische ondersteuning bij de uitvoering van het experimentele werk, evenals Benny Brouwer bij het structureren van de gegevensopslag. Mijn waardering gaat uit naar de medewerkers van de proefaccommodaties 'de Ossekampen', proefaccommodatie 'de Haar' en de laboratoria en bibliotheek van Zodiac. Gedurende het onderzoek heb ik gebruik kunnen maken van faciliteiten en apparatuur van het IVVO te Lelystad, onderzoekscentrum 'Het Spelderholt' te Beekbergen en het slachthuis te Veenendaal, waarvoor dank.

Met name wil ik ook noemen de studenten en stagiaires die hebben geparticipeerd in het onderzoek: Gerard de Bruin, Pieter Reitsma, Hans Leneman, Jeroen Veraar, Gabby Odekerken, Peter Verschoor, Pienie Vermeer,

Herman Koopman en Walter Jansen. De mogelijkheid die Henk Udo mij bood tot een flexibele werkindeling bij mijn aanstelling in de MSc-cursus Animal Science en zijn betrokkenheid heb ik bijzonder op prijs gesteld. De hulp en belangstelling van mijn overige collega's van de sectie Tropische Veehouderij en de ontspannen werksfeer waren een belangrijke steun in de rug.

Het uitvoeren van een promotie-onderzoek is tot op zekere hoogte een behoorlijk asociale en egocentrische bezigheid, waarbij heel veel gevraagd wordt van je naaste omgeving. Marja, jouw constante steun en geduld zijn van onschatbare waarde geweest.

CONTENTS

GENERAL INTRODUCTION

GENERAL INTRODUCTION

Genetic size

The genetic size of an animal is the major genetic factor that controls rate of growth from early embryonic stage to full maturity, and continues to determine rate and duration of life processes during the remaining part of life (Taylor, 1980). Genetic size is expressed at all developmental stages of growth, but is most clearly visualized by the size of the mature animal; usually genetic size is quantified by this adult weight. Basically, genetic size represents *the scale of the standard life programme* that species have in common within their main taxonomic group (like mammals or birds). This common genetic growth programme determines the animal's design from conception to maturity. The gene complex that embodies the genetic size factor, governs both the scale of size in this growth programme, and the time scale of development toward maturity. The consequences of the genetic size scaling factor can be best demonstrated and understood by comparing the growth and production of species that differ widely in adult size.

As an example, two related ruminant species are compared: goats and cattle. Their difference in scale is expressed from birth onwards to adult weight, cattle being about 10 times larger at equivalent stages of development. Goats reach sexual maturity at a much younger age than cattle. Similarly the gestation length of goats (145-150 days) is much shorter than of cattle (about 280-290 days). As a result the first parturition takes place at an age of about one year in goats and two years in cattle. Of course daily milk yields of goats are much lower. The performances of the best dairy breeds of both species show that cattle do produce less than the tenfold yield of goats, which might have been expected from their weight ratio. This implies that, per unit weight, goats generally produce more milk. But goats also appear to eat more food per unit weight. As a result the efficiency of food utilization for producing milk is on average the same, as already observed some 50 years ago by Brody (1945). The mentioned differences may seem to be the random result of some haphazard factors. Yet, this case exemplifies a systematic pattern of general scaling relationships, which all can be derived from their difference in genetic size, as will be outlined below.

Since the last century, biologists have been aware of these characteristic differences between large and small species. In a gradual process of expanding biological knowledge and increasing availability of data from various species, many relationships have been clarified and formalized. A major achievement was the introduction in 1932 of the concept of metabolic weight by Kleiber, followed in the same year by Brody and collaborators (Kleiber, 1961; Brody, 1945). They found that variation in metabolic rate between adults of different species is proportional to their metabolic weight, which is usually calculated as $(\text{liveweight})^{0.75 \text{ or } 0.73}$. Another major breakthrough was the introduction of the genetic size scaling theory by Taylor (1980, 1985). Taylor integrated the existing knowledge on scaling in a comprehensive theory, in which he introduced the concept of genetic size and two formal scaling rules. In essence this theory states that variation between animals can to a large extent be explained by differences in scale, expressed by the factor genetic size. By applying the scaling rules, the differences in scale can be eliminated. What remain are size-independent differences.

Briefly, the scaling rules state that input and output variables which are expressed per time unit, like daily food intake and milk produced, have to be scaled (i.e. divided) by the adult weight raised to the power 0.73 ($A^{0.73}$). Time spans of specific biological events, like gestation, have to be scaled by $A^{0.27}$. On basis of the ratio of A in the goat-cattle comparison and the scaling rules, the following ratios are expected in this example: for daily input-output variables, ($A^{0.73}$goat/$A^{0.73}$cattle) = $10^{0.73}$ = 5.4, and for time spans, $10^{0.27}$ = 1.9. So the daily milk yield of cattle is expected to be 5.4 times larger than those of goats. This would imply that per unit weight goats produce almost two times more than cows. The expected ratio for the gestational lengths (1.9) is in line with the actual ratio of both indicated ranges which is approximately 1.9. An important implication of the scaling rules is that ratios of input and output variables are size-independent as they have the same scaling factor ($A^{0.73}$). Hence Brody's observation of equal food efficiency for milk production is in accordance with the expected independency of size.

Genetic size scaling in breeding

The size scaling theory may be very useful for animal breeding. The theory provides a biological basis for explaining genetic variation within and between different taxonomic levels of mammals or birds, i.e. among individuals, groups of individuals within species, species, genera, families and so on. Practical animal breeding in current animal production systems is normally restricted to utilizing genotype variation within species, selecting the best individuals within a breed, or in some cases taking the most promising breed. In general, breeding strategies aim at selecting the biologically most efficient animals, with high overall feed efficiencies for their type of production. In this breeding goal there is very often no need for changes in size, as this trait is not correlated with biological efficiency. Changes in size may sometimes even be undesired if there is a risk that size-related management and market standards are exceeded. Application of the size scaling rules, in principle, enables a separation of variation due to genetic size and size-independent variation.

A classic example of breeding effects that can be explained by indirect selection on genetic size can be found in broiler production. For many years birds have been selected for high growth rate, high feed efficiency and high lean proportion at a fixed slaughter weight. What actually happened was that genetically larger sized animals were favoured (Rickleffs, 1985). When compared at equal weight, genetically large animals grow faster than genetically small animals. At equal weight, larger sized animals are physiologically less mature, being at a lower proportion of their mature weight than smaller sized animals. Both feed efficiency and lean proportion tend to decrease as animals mature. Thus, the effect of a lower degree of maturity on feed efficiency and lean proportion again favoured selection of large sized animals.

This example shows that an increase in genetic size may help to improve feed efficiency and body composition if animals are selected at a fixed slaughter weight. This improvement is only the result of a lower degree of maturity at slaughter. Not all size effects, however, turned out to be beneficial for broiler production. Parental stock has become very large sized and expensive to maintain. If breeders would have been aware of the genetic size effects, they could have avoided undesired effects by using size-independent traits. Parental

stock would have stayed smaller, but the price to be paid would have been a slower progress in improving feed efficiency and lean proportion as no longer the degree of maturity at slaughter can be reduced.

So far the concepts of size scaling have hardly been adopted in current breeding practices. Despite a better understanding of the biological basis of production efficiency, breeding remains to be mainly practised by selecting fast growing animals for meat production (Barlow, 1984), and high yielding animals for milk and egg production (Korver, 1988; Luiting, 1991). These traits are positively correlated with genetic size. In case of meat production, size effects may be favourable, as outlined before. In case of milk or egg production, however, size does not affect the feed efficiency for production. Including a size component in selection traits reduces the selection pressure on biological efficiency (Taylor, 1985). If it would be possible to define size-independent traits for high production yields, selection on feed efficiency would become more effective.

The apparent neglect of the size scaling concepts in breeding does not arise from a lack of interest in efficient animals. On the contrary, in view of the limited market possibilities for animal production in many Western countries during the last decade, an increasing attention has been given to reducing feed costs (Korver, 1988), which can be achieved by improving the genetic basis for biological efficiency in animals. The main reason for lack of adoption of the genetic size concept is that there is no adequate measure of genetic size available, on which individual selection can be based. The importance of genetic size variation within breeds is therefore difficult to evaluate, and as such provides no compelling reasons for including size scaling concepts in breeding practices.

Breed evaluation in tropical animal production systems

Tropical animal production systems are (still) characterized by a very large variety of breeds within farm species (Mason, 1988), which differ widely in mature size. During the last few decades, increased population pressure in many tropical regions urged for a further intensification and commercialisation of animal production. To overcome, what is considered by many to be, the poor genetic basis of livestock for productivity, attempts have been made to increase

low output levels by improving genotype. For ruminants, in particular cattle, this often resulted in importing exotic dairy and beef breeds for pure breeding or crossbreeding with local breeds.

This breeding policy was based on the belief of the 'superiority' of temperate cattle breeds in terms of high yields and growth rates, but overlooked environmental factors and the on average much larger genetic size of temperate breeds. Due to the entirely different environmental setting in the tropics many efforts ended in failure (Pearson de Vaccaro, 1990), especially in case of pure exotic breeds. It made clear that the so-called 'genetic potential', normally expressed as the upper limit of possible performance, has no meaning at all if environment is ignored. The genetic size scaling theory indicates that introducing larger sized breeds as such does not improve the biological efficiency of production. Nevertheless, crossbreeding schemes with large temperate breeds have been implemented in many countries, like India and Bangla Desh, and are bound to eliminate many local pure breeds (Maule, 1992). The significance of tropical indigenous breeds as valuable genetic resources is, however, increasingly more recognized (Brem *et al.*, 1989).

Despite the increasing interest in indigenous livestock, breed evaluation schemes of tropical ruminant breeds are relatively scarce (Hetzel, 1988). The few comparative studies that were undertaken ignored genetic size effects, or corrected for them inadequately. For example cow productivity is normally calculated as yearly weaned weight plus the liveweight equivalent of milk produced per 100 kg of cow weight (FAO/ILCA/UNEP, 1980). Such a procedure tends to overvalue small cows because their production level per kg weight is higher as a result of their smaller size. As long as size variation is relatively moderate, such evaluation criteria may be useful, but for instance in crossbreeding schemes with small and large breeds modified criteria are required. Introducing the concepts of the size scaling theory in breed evaluation schemes can be very fruitful; better criteria for breed evaluation can be applied, and a better insight is acquired in the true value of different sized breeds.

The objectives of this study

In view of the promising perspectives of utilizing scaling concepts in evaluation of genotypes on one hand, and the problems associated with practical implementation on the other, this study has been undertaken in an attempt to solve some of the implementation problems. The main objectives were:

1. To improve the practical applicability of the genetic size scaling theory at the individual genotype level and at the breed level. The study particularly focused on exploration of alternative measures for genetic size.

2. To elaborate methods for evaluation of growth characteristics among individual genotypes and breeds which incorporate the genetic size concept, and which enable assessment of the relative importance of genetic size in breed differences.

In order to meet these objectives a long term experiment with two goat breeds was designed and carried out.

The growth experiment with two goat breeds

For two goat breeds, data on growth, *ad lib* feed intake, body composition and body frame development of castrated males were recorded during 3 years (1987-1990) from birth to a weight level near the asymptotic weight. The two goat breeds used in the trial differed widely in adult size: the Saanen breed, a large sized European dairy breed, and the West African Dwarf goats (WAD goats), one of the smaller goat breeds. Their strong contrast in size was considered useful for studying genetic size effects.

On the premise that alternative genetic size measures might be derived from 'landmarks' in growth patterns of components relative to other body parts, special attention was directed at obtaining data on changes in body composition and development of external measurements. A serial slaughtering scheme was designed to examine the changes in body composition.

Nutritional effects on growth patterns are of special interest in relation to possible measures of genetic size. What is required for an adequate genetic size

determination is a measure that is not easily changed by environmental effects. Feed quality is such an important environmental element and was therefore included as a factor in the experiment. Within the WAD breed, half of the animals received the same standard diet as the Saanen breed, and the remaining half a diet of a much lower quality. The effect of feed quality on growth patterns could be used to assess the suitability of possible measures for genetic size.

Contents of the thesis

The general introduction of this thesis is followed by six chapters and general conclusions. All chapters were written with the intention to stand on their own as independent papers. In the first chapter, literature on size scaling is presented and discussed. The other chapters deal with analyses and concepts based on results of the growth experiment.

Chapter 1 of this thesis starts with a brief overview of the main developments in the study of metabolism and scaling since the last century. An outline is given of the scientific progress since the early surface law, the introduction of the genetic size scaling theory and its possible applications in animal production. This outline serves to describe strengths and weaknesses in our current knowledge of scaling relationships and to identify areas where additional basic research is needed for successful application in practice.

An integrated feed intake and growth model is presented in Chapter 2. On basis of the presented model, data of the growth experiment were analyzed. The proposed approach enables analysis of the effects of breed, their genetic size and feed quality on growth and feed intake. This chapter gives a detailed description of the long term experiment. It describes animal management, feed composition, digestibility experiments and other experimental methods related to the recording of feed intake and growth.

The next three chapters focus on allometric growth patterns of body components (relative to fatfree weight or liveweight) and the effects of breed and feed quality on them. Relationships between allometric growth characteristics and genetic size are examined. Allometric growth of a number

of body components in the experiment showed phasic patterns. The chapters, therefore, were all based on multiphasic analysis of allometric growth. Parameters from multiphasic models are shown to be of interest as characteristics for determination of genetic size.

Chapter 3 and 4 are based on cross-sectional slaughter data of the experiment, which ranged from birth to body weights near the asymptotic weight level. In Chapter 3 the phasic development of chemical body components relative to fatfree weight is described. The development patterns of a number of organs is described in Chapter 4. Chapter 5 is based on multiphasic analysis of individual longitudinal data sets. In this chapter the development of body dimensions relative to liveweight is analyzed.

In Chapter 6, the results and conclusions from the foregoing chapters are discussed in view of the formulated central objectives. Determination methods of genetic size characteristics are discussed. Measures of these genetic size characteristics are compared and their practical suitability judged on basis of the criteria outlined in Chapter 1. The conclusions of preceding sections are summarized and their implications and prospects for use in genotype evaluation briefly discussed. Finally, the major findings of this thesis are summarized in general conclusions.

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CHAPTER 1

GENETIC SIZE AND THE ANIMAL METABOLISM: DEVELOPMENTS, APPLICATIONS AND CONSTRAINTS

ABSTRACT

The allometric equation ($Y = aW^b$) has been shown in literature to be very effective in explaining between-animal variation of metabolism variables (Y) as a function of weight (W). Here the change of Y relative to W is called the 'scaling' of Y to W. This chapter describes briefly the main developments in the study of scaling patterns in animal metabolism, from the surface law, the mouse-to-elephant curve, to the genetic size scaling theory of Taylor. The scaling theory generalizes and integrates the size-metabolism relationships for different variable types. The theory may be useful in animal production as animal variation due to genetic size can be separated from size-independent variation.

Two basic problems are identified in this chapter in applying the genetic size-scaling theory at a practical level: rules for intra-specific scaling are not firmly established, and a practical accurate method for size determination is lacking. Conditions for an ideal practical measure of genetic size are formulated, and current methods for size determination in ruminant species are discussed. It is concluded that a promising approach for determination of genetic size might be to look for characteristics in (relative) growth patterns of body components that are linked to functional stages of development. To select such promising alternatives more detailed knowledge is required of allometric growth patterns.

GENETIC SIZE AND THE ANIMAL METABOLISM: DEVELOPMENTS, APPLICATIONS AND CONSTRAINTS

INTRODUCTION

Modern research in animal metabolism started in the 18th century with the discovery by Lavoisier of the role of an 'acid forming' substance, called oxygen, as an essential element for the 'fire of life' of living beings (Kleiber, 1961). He found that both the flame and the animal consumed oxygen and as a result produced heat, water and carbon dioxide. This major breakthrough was soon followed up by respiration calorimeter trials to quantify the animal's metabolism. Since then an ever increasing number of experiments have been carried out, elucidating step by step the utilization of oxygen and food energy for growth and other life-essential functions.

From the early beginning on, quantitative relationships between animal size and metabolism have received considerable attention. It soon became apparent that the scaling of metabolism was in a particular way related to size. Research workers in the field of animal production played a significant role in clarifying the basic patterns in scaling relationships. The remarkable work of Samuel Brody, compiled in his *magnum opus* 'Bioenergetics and Growth' (1945), is especially mentioned here as a milestone of conceptual development in this area. The work of Brody exemplifies an era in which fundamental biological sciences and animal science were more integrated than now and mutually benefited from the heterosis of integration of knowledge. The apparently inevitable trend of further specialisation in ever narrowing disciplines, especially notable during the last few decades, has unfortunately resulted in a loss of this synergy. Fragmentation of knowledge in animal science and a concomitant bias toward strictly applied problem solving is nowadays posing a serious threat to maintaining depth and developing new concepts.

The aim of this chapter is to give a brief outline of the main developments in the study of scaling of metabolism, from the early surface law to the genetic size scaling theory, and its possible applications in animal production. This outline serves to describe strengths and weaknesses in our current knowledge

of scaling relationships and to identify areas where additional basic research is needed for successful application in practice.

For ease of reference a classification of different types of variables that are involved in the animal's metabolism will be given first. This is followed by a short explanation of the allometric equation, which is widely used in scaling studies. After this, a brief historical overview of the study of scaling is presented, followed by an introduction to the genetic size scaling theory. The final section discusses the theory's scope for practical applications and its current limitations.

TERMINOLOGY OF VARIABLES AND ALLOMETRY

Classification of variables

Parks (1982) offers in his book 'A theory of feeding and growth of animals' a useful framework for a simple classification of variables. Parks argues that analysis of animal growth should be based on considering animals as a dynamic system with input and output. He therefore advocates an integrated analyses of the main relationships in such a system, contrary to classical growth studies which primarily focused on weight-age relations. In a dynamic input-output system we can distinguish three groups of cumulative variables (Figure 1):

1. Cumulative input-variables (I), like total food consumed or cumulated oxygen consumed (*cumulative* indicates here cumulation from conception until the present state).
2. Cumulative output-variables (O), cumulated growth or weight being the most important one.
3. Cumulative time (T), or age.

From these three groups we may define variables which are based on the derivatives of the cumulatives (Figure 1). All variables of the type dI/dT or dO/dT are called here *rate* variables, so daily feed consumption and growth are rate variables. Variables based on dO/dI are called hereafter *efficiency* variables.

As will be demonstrated later this classification scheme is very useful for the understanding of scaling relationships.

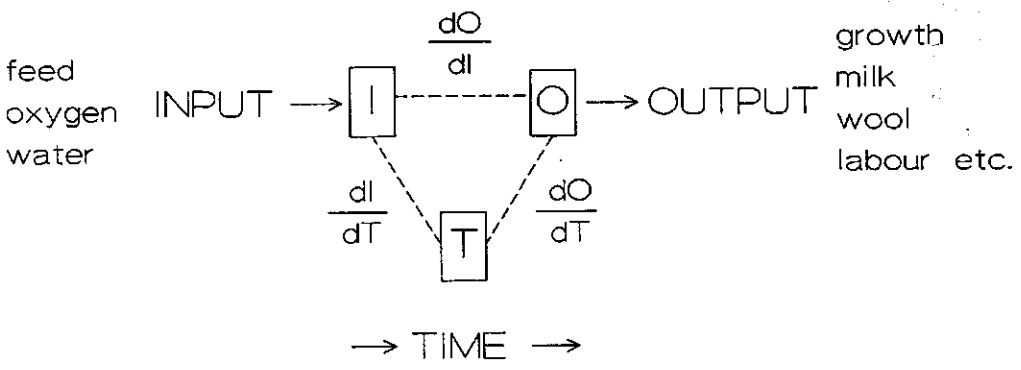

FIGURE 1. *Variable types involved in the animal's metabolism: cumulative variables (I,O,T), rate variables (dI/dT, dO/dT) and efficiency variables (dO/dI)*

The allometric equation

The following power function has been proven to be very effective in describing relationships between an animal's characteristic (Y) and its weight (W):

$$Y = aW^b$$

The pattern of change in Y relative to W is called *isometric* if the ratio between Y and W remains constant; this occurs for $b = 1$, where $Y/W = a$. If $b \neq 1$, this pattern of change is called *allometric* (from 'allos' which means 'other'). Because the latter is usually the case in biology, the power function is normally termed the *allometric equation*. The allometric equation can be transformed into a linear form by taking the logarithm of the power function:

$$\log(Y) = \log(a) + b \log(W)$$

Here we see that the parameter b represents the slope of the linear relationship between log(Y) and log(W). The allometric equation has been widely used in biology ever since Julian Huxley (1924) demonstrated its usefulness as a tool for analyzing relative growth problems. By differentiating both sides of the

equation we may see that the (dimensionless) parameter b can be interpreted as the ratio between the relative or specific growth rates of Y and W:

$$(\frac{dY}{dT} \cdot \frac{1}{Y}) = b\ (\frac{dW}{dT} \cdot \frac{1}{W})$$

Parameter b, therefore, is very often referred to as the *relative growth coefficient*. The allometry of relative growth is usually called *ontogenetic* or *growth allometry*, because the variation in Y is due to differences in growth stages during an animal's development (ontogeny). Besides growth allometry we can distinguish *static allometry* and *evolutionary allometry* (Lande, 1985). In static allometry we compare Y among different-sized adults or otherwise individuals that are at the same stage of development. If individuals are from different species, this allometry is called *inter-specific allometry*, whereas for within-species variation this is called *intra-specific allometry*. Evolutionary allometry studies variation in Y as a result of evolutionary changes. It should be noted that growth allometry and static allometry are fundamentally different in nature and should not be mixed up. It is the static form of allometry that essentially deals with size scaling, as it is based on variation due to differently sized individuals. Here the change of Y relative to W^b is called the 'scaling' of Y to W^b. In static allometry, parameter b therefore is called the *scaling coefficient*.

In fact it was the static form of allometry that was initially used in biology. In 1891 Snell described the inter-species scaling of brains within taxonomically different groups of mammals (Brody, 1945; Gould, 1966). Snell claimed that parameter b was similar among different taxonomic groups. The ratio of their intercepts (a) therefore, should equal the ratio of brain weight at any given body weight. For this reason parameter a was initially called the 'cephalization' factor by Snell (Brody, 1945), which fortunately appeared to be highest in man. Despite their high 'cephalization' factor, many biologists have misinterpreted parameter a since then, as they did not realize that Snell's interpretation of parameter a only makes sense in the special case of equal b (Gould, 1971). As will be described in the next section it took another 40 years before the allometric equation was put to effective use by Kleiber and Brody for scaling of metabolism.

FROM SURFACE LAW TO THE MOUSE-TO-ELEPHANT CURVE

Size and metabolic rate

A multitude of closely interlinked variables that are involved in the catabolism and anabolism processes can be categorized as metabolic rate variables. Relationships between size and metabolic rate variables have been studied since the 19th century. Among these, especially respiration variables have traditionally received much attention, as respiration is the key-process in producing energy for essential functions throughout the individual's life history.

Early researchers already found that the heat production per unit weight was higher for small animals compared to big ones. Sarrus and Rameaux presented a thesis in 1837 in which they argued that heat production of warm-blooded animals should equal their heat loss (see Brody [1945] for a historical review of respiration research). It was assumed that heat loss was proportional to body surface, therefore heat production was also proportional to body surface or the two-third power of their weight ($W^{2/3}$), an argument which became known as the surface law. Similar considerations led a decade later to the formulation of Bergmann's rule which stated that individuals of homoiothermic (warm-blooded) species tend to be larger in cooler areas and that among related species the bigger ones are to be found in cooler climates.

For about a century, theories and explanations related to metabolic rate were almost exclusively dominated by the surface law. In 1932 both Kleiber and Brody & Proctor rejected body surface and the related $W^{2/3}$ as a reference base for metabolic rate (see Brody [1945] and Kleiber [1961] for their original publications). They instead proposed to use as a reference base, what Brody (1945, p.363) later called 'noncommittal *physiologically effective* body size represented symbolically by W^b, the value of the exponent b to be determined by actual data'.

In the 1932 publication Kleiber concluded that the 3/4 power of W provided the right reference base. He based this finding on plotting logarithmic data of daily fasting heat production *versus* mature weight of different bird and mammalian species, ranging in size from dove to steer. On this log-log plot a strong linear

relationship appeared (Figure 2). Linear regression on data of the 10 mammalian species included showed a slope of 0.739 and a residual standard deviation of only 0.03 logarithmic units, which corresponded to a coefficient of variation of about 7% (Kleiber, 1961). Somewhat later in the same year Brody and Proctor calculated an inter-specific coefficient of 0.734 for fasting metabolism data of mammalian species. In a subsequent analysis two years later Brody and collaborators arrived at exactly the same value from an extended data set of mammalians which became known as the 'mouse-to-elephant curve'.

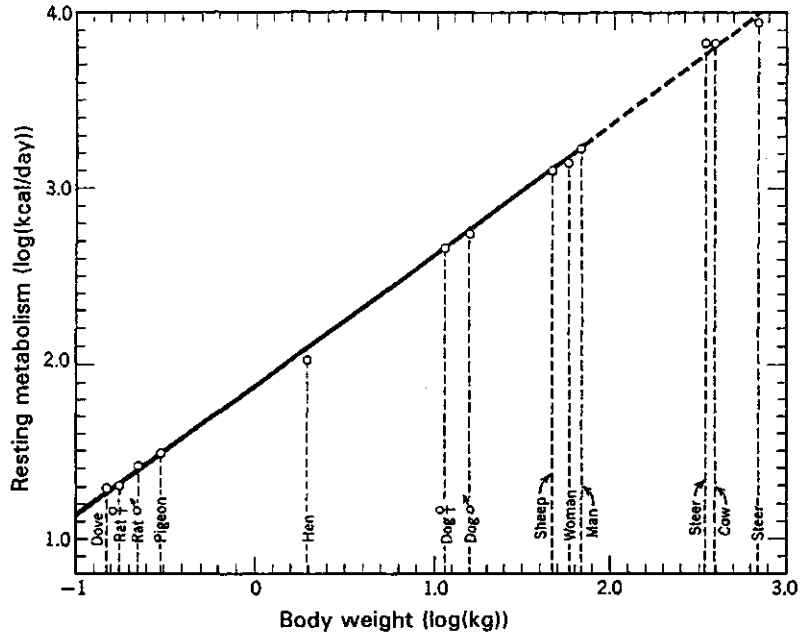

FIGURE 2. *The first published representation of the 0.75 scaling coefficient for rate variables by Kleiber in Hilgardia, 6:321 in 1932*

There has been quite some discussion in literature about which particular scaling coefficient should be adopted, without a clear agreement and several scaling coefficients have been used since then. It is worthwhile to note Kleiber's argument (1961, p.212) that, given the high coefficient of variation in metabolic rate per unit size in the mouse-to-elephant range, it is statistically impossible to decide on a specific two-decimal coefficient. Yet it is clear that

this coefficient has an approximate value around 3/4 and evidently deviates from 2/3. Kleiber therefore preferred the notation 3/4 as this value lies within the observed range of coefficients and could easily be calculated by a slide-rule. One might argue, however, that use of the fractional expression '3/4' is suggesting an unjustified high accuracy. In current literature the decimal notation '0.75' has generally been accepted as the standard expression; for reasons of uniformity in this thesis the 0.75 notation has also been adopted.

Abandoning the reasoning of the surface law gave way to a new series of explanations for the empirical relationship between metabolic rate and size. Extensive reviews on this subject are provided by Brody (1945), Kleiber (1961), Peters (1983), Calder (1984) and others. All concluded that no convincing clear-cut explanation had been presented sofar. The many attempts to explain the 0.75 coefficient may have arisen from the remarkable general validity of the 0.75 exponent among taxonomic very divergent groups. Many biologists believed that a basic biological law should underlie this phenomenon. Both within unicellular organisms, poikilotherms and homoiotherms this scaling coefficient was demonstrated to be valid. Reiss (1989) listed equations for these different groups of standardized metabolic rate (MR, in watts) against weight (W, in kg), which he adopted from the work of Hemmingsen who collected a very extensive data set from literature:

homoiotherms: $MR = 4.1\ W^{0.739}$
poikilotherms: $MR = 0.14\ W^{0.738}$
unicellulars: $MR = 0.018\ W^{0.756}$

The similarity of the scaling coefficient is striking. The equations also show a considerable difference in metabolic rate per unit $W^{0.75}$ which has to be related to the entirely different ways in which these groups function physiologically. These equations may be seen as an illustration of the comparative power of allometric relations in general, as they enable a clear distinction between aspects in which groups are similar and other aspects in which they essentially differ.

Another reason why there has been such a wide interest in the scaling coefficient 0.75 and its possible explanation, is that next to respiration variables other rate variables, related to the metabolism, also appear to scale accordingly. There is general agreement in literature that both intake and output rate variables have the same scaling coefficient of 0.75 within their main taxonomic level (see for a more detailed discussion of the very extensive literature on these allometric relationships Peters [1983], Schmidt-Nielsen [1984], Calder [1984]). This consistency in scaling patterns reflects an important principle in biology which at the beginning of this century was called by D'Arcy Thompson 'the principle of similitude' (Thompson, 1961) and was later also referred to as 'biological similarity' (Stahl, 1962). As will be shown in the next section biological similarity plays a dominant role in relationships between intake, growth and time. Since the majority of relevant data were obtained from mammals and birds, studies of similarity aspects in literature are normally restricted to these taxonomic groups. The same therefore also applies to the following section on biological similarity.

Biological similarity

In his papers on similarity and dimensional methods in biology, Stahl (1962, 1967) explained how nondimensional combinations of variables may serve as a criterion of similarity for systems differing in scale, and more in particular for species of different size. By making use of known allometric relations from mammalian biology he showed that a number of dimensionless ratios appear to be virtually independent of animal size. For example, he showed from data in literature that the rate variables, oxygen flow and renal inulin clearance (both in m^3t^{-1}) can be described as a function of animal size (M) by the allometric equations $3.8M^{0.73}$ and $1.74M^{0.77}$. Hence their dimensionless ratio, relating lung to kidney functions, is related to M as $2.2M^{-0.04}$, which means that a fairly constant ratio close to 2.2 can be found in both small and large mammalian species. As the equations for both rate variables are empirically derived, there is some unavoidable error in estimating their scaling coefficients. The power value of 0.04 therefore has the same uncertainty and does not necessarily imply a statistically significant effect of size on this ratio.

A large series of ratios can be defined from the rate variables involved in the overall metabolism, that reflect the functional relationships between input and output processes. As all these variables have a common scaling coefficient close to 0.75 their ratios will as a rule be independent of size. It means for instance that the ratio between energy intake and energy retained in output variables, like milk, is in general the same for mammalian species of different size, i.e. the conversion efficiency of energy is size-independent. Similarly fasting heat production and *ad lib* energy intake show, on average, the same ratio irrespective of size. The size-independent nature of these ratios have to be the result of a common basic design and physiological functioning.

Relationships between rate variables and size of animals, traditionally, have been mainly based on data from *adult* animals to avoid complications due to differences in developmental stage (ontogenetic variation). Biological similarity however is not restricted to this specific stage in the animal's life history, nor is biological similarity reflected by ratios of rate variables only. We may widen the similarity concept to static comparisons at other equivalent ontogenetic stages, and other types of biological variables, in particular time interval variables.

To do so, one first needs to identify similar stages that may serve as reference points for a meaningful comparison across genotypes. In the mammal's life history for instance, we can distinguish common stages like conception, birth, weaning or sexual maturity. But other minor ontogenetic stages also can be distinguished, which all mammals have in common and have to go through. Similarly bird species have their own general life plan marked with common stages of development. The time spans between these specific ontogenetic events (here called maturation intervals) appear to be positively correlated with size. As will be outlined below, maturation intervals also scale allometrically with body size. It will be demonstrated how scaling of maturation intervals is related to the scaling of rate variables, and in particular to an important variable in growing animals: growth rate.

Physiological and metabolic age

It is well established that, across the mice-elephant curve, maturation intervals increase as species increase in size. Brody (1937) was the first who analyzed in a systematic way physiological time during growth of mammals and birds. He found that for many species growth beyond puberty could be well described by the curve $W = A(1-\exp^{-k(t-t^*)})$, where W is weight at age t, parameter A represents the asymptotic W, t^* the time origin of the curve, and k the time scale of maturing toward A as will be explained hereafter. Brody called $k(t-t^*)$ 'physiological age' as it represents the standardized age at a given stage of development characterized by W/A, assuming that species are equally mature at a given proportion of A. So when animals reach a stage of development W_1/A at t_1 they all have the same 'physiological age' $k(t_1-t^*)$. It can be easily seen that standardized maturation intervals corresponding to W_1/A-W_2/A are equal to $k(t_1-t_2)$. This means that the time (t_1-t_2) required for a specific maturation interval is standardized by the unit 1/k. In other words, the reciprocal 1/k can be interpreted as a time scale unit of maturation for a given species.

Brody (1945) noticed that mature size A tends to be related to k, and therefore to time required to reach a given percentage of A. However, he quantified this relationship in a rather unfortunate way by regressing log(A) on the logarithm of time required for the 0-98% interval of A ($t_{0.98}$). Günther and Guerra (1955) used the parameter estimates from Brody's growth curves but now the other way round. They regressed the log-values of two calculated maturation intervals ($t_{0.50}$ and $t_{0.98}$) on log(A), and found regression coefficients of respectively 0.245 and 0.255, almost similar values close to 0.25. An important implication is that scaling coefficients are nearly the same for partially different sections of the growth curve, suggesting one common time scaling unit of $A^{0.25}$. Stahl (1962) utilized this ratio $t_{0.50}/t_{0.98}$ as an example of a size-independent criterion of similarity in mammals. Neither Brody, nor Günther and Guerra further elaborated the relationships between the scaling coefficients of time variables and rate variables.

Taylor (1965, 1968) was the first who clarified the link between scaling of rate variables and time variables. He developed and generalized the concept of one

uniform time-scaling unit for maturation intervals. Taylor (1965) derived an empirically based inter-specific relationship between A and maturation time by making use of the extensive work of Brody (1945) and Weinbach's (1941) study on pre-natal growth. In both these studies, growth was described by scaling parameters for liveweight (A) and age (1/k), and an age origin parameter. By regressing log(1/k) on log(A) Taylor concluded that maturation time (i.e. time to reach a given proportion of A) was proportional to $A^{0.27}$. This scaling coefficient, as Taylor noticed, enabled integration of the time-scaling concept for maturation and Kleiber's (1961, p.213) concept of metabolic time.

Earlier Kleiber (1961) defined metabolic time as 'the time in which large and small animals change the same proportion of their respective metabolic pools'. He deduced from the proportionality of pool size to W^1 and of metabolic rates to $W^{0.75}$ that metabolic time should be proportional to $W^1/W^{0.75} = W^{0.25}$, because turnover time is equal to the ratio of pool size to transfer rate. Hence maturation time and metabolic time have a scaling coefficient of similar magnitude, with the only difference that the former is scaled by A and the latter by W. For adult animals (to which Kleiber is referring) there is of course no difference as W equals A in this particular case. Intervals of metabolic time *during the process of maturation*, however, might as well be scaled by $A^{0.25}$ if we demand that species may only be compared at *equivalent stages of development*. If we assume that such equal stages should correspond to equal proportions of A, it follows that we also may scale by $A^{0.25}$, because we may substitute $W^{0.25}$ by $cA^{0.25}$, thus:

metabolic time = $aW^{0.25}$ becomes
metabolic time = $acA^{0.25}$.

Similarly, rate variables might as well be scaled by $A^{0.75}$ instead of $W^{0.75}$ at equal stages of maturity.

Because of the common properties of metabolic time and maturation time, Taylor introduced 'metabolic age' as an expression for scaled maturation time (using the scaler $A^{0.27}$) as this age scale 'amalgamates the properties of Brody's physiological age and Kleiber's metabolic turnover time' (Taylor, 1965). The

advantages of this age scale compared to Brody's physiological age are, that one parameter A is used for scaling instead of two (k,t^*) and that a relation is established with the scaling properties of metabolism rate, on basis of mature size A.

A crucial assumption, using parameter A as a single scaling unit for rate and time variables, is that specific ontogenetic events and their intervals should correspond to similar fractions of A among species. This implies that A^1 should act as the scaling unit for the cumulative variable W. Given this assumption it can be easily seen that the scaling coefficients for time and rate with regard to weight are complementary because growth rate can be written as $\Delta W/\Delta t$, where $\Delta W = aA^1$ and $\Delta t = bA^{0.25}$, so $\Delta W/\Delta t = abA^{1-0.25}$. Taylor's empirical result of a scaling coefficient close to 0.25 for maturation intervals of W (based on fractions of A) therefore meant that the inter-specific scaling coefficient for growth rate at any fraction of A should be 1-0.25 = 0.75, a value similar to those generally found for rate variables in adult animals.

Besides time intervals for specific fractions of A, literature shows that time spans related to stages in life history, like gestation length, age at reproductive maturity or maximum life span, also have scaling coefficients close to 0.25 (Lindstedt and Calder, 1981; Calder, 1984; Peters, 1983). This consistency with A-based maturation intervals supports the assumption that developmental stages should be directly related to proportions of A. It is of interest to note that many other time spans of cyclic physiological events scale accordingly, even if they do not represent any direct ontogenetic change. Adolph (1949) provided a set of allometric relationships for some cycle times like breathing, heartbeat and peristaltic gut movement with scaling coefficients close to 0.25. Given the same scaling coefficient for maximum life span it thus appears that, for each animal, life contains about the same number of cyclic events. Or as Calder (1984) stated 'each animal lives its life faster or slower as governed by size, but accomplishes just as much biologically whether large or small'.

The conditional basis of the before mentioned type of reasoning has to be emphasized. What is normally implicitly assumed is that these allometric time equations, which were mainly derived from adult animals, also apply for

relationships between growing animals. There are good reasons to support this assumption, but still a good deal of empirical evidence needs to be collected. How easy ontogenetic aspects are overlooked, may be demonstrated by the rather popular fashion of calculating numbers of heartbeats and breath cycles during the lifetime of a mammal (Stahl, 1962; Gould, 1979; Peters, 1983). All these calculations are based on dividing average lifespans by the average time adults need for a heart beat or a breath cycle, without taking into account the much shorter cycle lengths associated with higher metabolism rates during ontogeny. Such calculations thus tend to underestimate the real total number during lifetime.

THE GENETIC SIZE SCALING THEORY

Scaling rules and their implications

In a further development of his work on metabolic age, Taylor generalized the size-metabolism relationships into a set of scaling rules called the genetic size scaling theory. This theory makes it possible to exploit the biological information on size effects in the animal science discipline. Moreover, it integrates the scaling knowledge derived from relations between adult animals, into a wider framework that includes scaling effects at any stage of growth. The central premise is that all genotypes possess an inherent *genetic size factor* (quantified as mature size, A) that governs growth from conception throughout the subsequent stages of development to full maturity. The scaling effects on growth and metabolism, as outlined before, can be attributed to this single genetic size factor. The basic concepts of the theory can be summarized as follows (Taylor 1980a, 1980b, 1985):

I. genotypical variation can be separated into two main components. Variation due to genetic size A of an animal and the remaining (size-independent) genotype-specific variation. Genetic size differences are corrected for by applying the size scaling rules, leaving the normally more important typical variation for utilisation in breeding.

II. two formal scaling rules can be formulated (Taylor, 1980a):
1. scale all age (starting from 3.5 days after conception) and time-interval variables by $A^{0.27}$. This will give metabolic age and standardized interval variables

2. at equal metabolic age, according to (1), scale all cumulated inputs and outputs by A^1.

Animal variation can be regarded as the combined result of three main sources of variation. Environment, maturation, and genotype. For a proper assessment of genotype therefore both environmental *and developmental* differences have to be eliminated. This is most easy done by comparing genotypes in the same environment and at an equal degree of maturity or metabolic age. As indicated in the theory, the resulting genotypical variation should be separated into size effects and typical effects for a meaningful interpretation.

The quantitative element in the theory is embodied by the scaling rules. The first scaling rule is the one developed earlier in the work on metabolic age (Taylor, 1965, 1968). In the second rule we see a generalization of the use of A^1 as the scaling unit for weight toward scaling *all cumulative variables* by A^1. Hence, variables like cumulated food consumed, oxygen used, heat produced or milk yielded all have to be scaled by A^1. This accounts both for adult animals as for growing ones. A direct result is that all rate variables based on these cumulative variables are scaled by $A^{0.73}$, generalizing thus the complementarity rule (1-0.23) for their scaling coefficient. (Taylor uses the scaling coefficients 0.27 and 0.73, being the empirical result of his analyses on time intervals. In a previous section the statistical problems related to the accuracy of these coefficients have been mentioned. In this thesis the coefficients 0.75 and 0.25 are preferred, unless special reference is made to Taylor's work)

The second rule of the scaling theory also implies that ratios between cumulated input and output variables are independent of size, as they have the same scaling unit. This means that the individual biological efficiency in the use of food for growth and other output purposes is considered to be independent of size. Again this may be seen as an extension from the already known

biological similarity in efficiency of energy use in adult animals toward growing animals. This assumption is a very crucial one with regard to the assessment of the overall biological efficiency of different sized species. The assumed size-independency of efficiency for growth finds support in the relatively scarce literature on the relation between (genetic) size and energy efficiency for growth.

At the beginning of this century Rubner concluded from experimental data that the amount of energy required for doubling the birth weight is the same per kilogram in all species, except man (Brody, 1945). Rubner's law is a special case of Taylor's generalization, as it refers to a limited part of the growth curve. Parks (1982) defined in his theory of growth a parameter (denoted AB) for the efficiency of food conversion in growth. Analyses, based on literature data, indicated that AB was not related to adult weight and showed, as Parks claimed, a remarkable consistency among species. Blaxter (1989) listed efficiencies for use of metabolisable energies in different sized species, which show a strong relation with the digestive system and feed quality but not with size. In an analysis of 235 energy budgets of different species, Humphreys (1979) found that the ratio between energy retained in production (growth and reproduction) and energy assimilated was independent of species weight within the main taxonomic groups. So far there are no literature reports known here which contradict Taylor's generalization. Yet this rule should not be considered as a fully evidenced fact; it needs a stronger empirical basis than data currently available can provide.

The mean standardized growth curve

If, for different genotypes, growth and age are standardized according to the scaling rules it is possible to construct a mean standardized growth curve, to arrive at what Taylor (1985) called a 'unified description of mammalian growth'. This curve may be considered as the most elementary representation of similarity of growth in mammals; a similarity based on a common genetic basis for the fundamental aspects of ontogenetic growth, which is shared by all species from small to large, from shrew to whale. Taylor (1980b) presents such a mean standardized curve together with the separate species curves based on literature data of eight domestic species (Figure 3a). The graph shows that

relatively slow (guinea pig) and fast maturing species (rabbit) can be easily distinguished by this procedure. Instead of metabolic age, time scale of such standardized mean graphs could as well be expressed as a percentage of the maximum life span, like Peters (1983) does (Figure 3b). This representation shows how important developmental phases (birth, sexual maturity, death) take place at similar proportions of an average mammal's life.

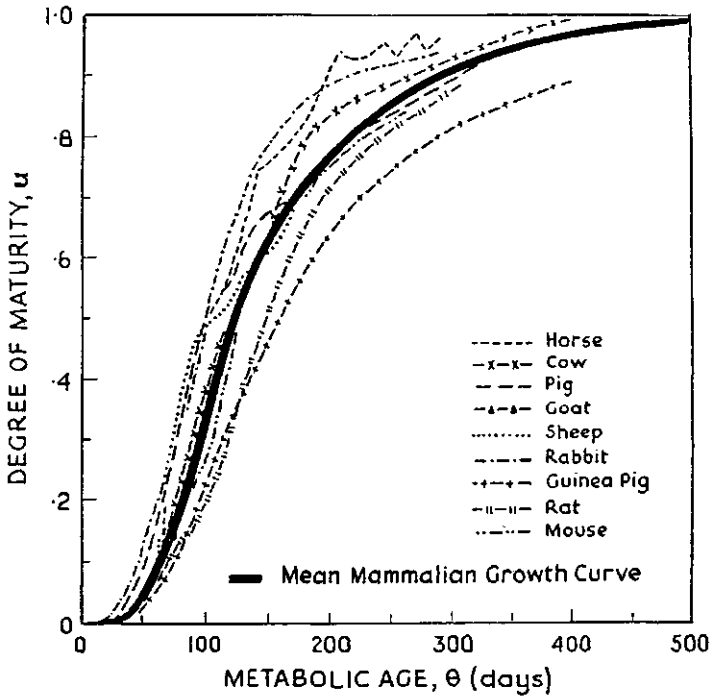

FIGURE 3a *The mean mammalian growth curve and the size-scaled curves for eight species, from Taylor (1980b)*

Without doubt the genetic size scaling theory and its methods have contributed in a very useful way to the evaluation of genotypes. In animal breeding, the theory in principle enables more efficient selection strategies among and within breeds by removing undesired size variation from traits. Instead of selecting animals with high milk yields or high growth rates aiming at higher biological efficiencies, one could correct these traits for genetic size to avoid correlated size increases, which bears no direct relationship with higher biological efficiency. Nevertheless it should be kept in mind that the main elements of this

theory are generalizations which should be subject to further validation, as more empirical data from genotype comparisons will become available. In particular, the lack of suitable coherent data sets so far has hampered a meticulous verification of the different elements of the theory. Besides verification, a number of application problems also deserve further attention. The next section will deal in more detail with a number of questions related to the application of the genetic size scaling theory.

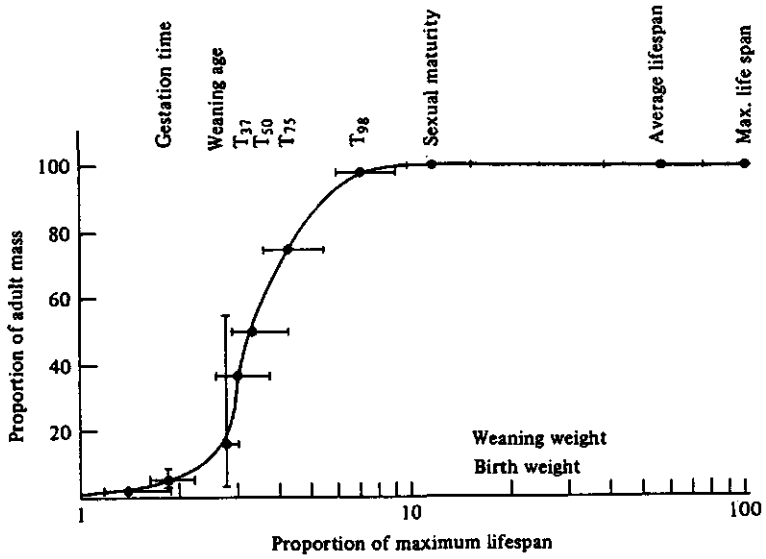

FIGURE 3b. *Generalized representation of the life history of eutherian animals, from Peters (1983)*

PROBLEMS IN APPLICATION OF THE GENETIC SIZE SCALING THEORY

Application in animal production

In animal production the main importance of the scaling theory lies in its application as a method to select the best breeds of a certain species, or the best individuals within a breed. Of course there is a biological interest to compare the growth performance of elephants with those of mice. For modelling purposes too it may be very useful to develop growth models based on standardized data of one species (like sheep) and to apply the model to other (ruminant) species by adjusting for the genetic size factor. In common animal

husbandry practice, however, species is a fixed factor that is firmly established in the production system and therefore is not easily interchanged. Here choices in selecting animals are restricted to those within a given species. In application of the scaling theory at this practical level we can identify two basic problems, which appear to be interlinked:

1. Rules for *intra*-specific scaling are not firmly established. There are some scaling relationships reported which suggest that scaling mechanisms might not be the same for inter-specific and intra-specific variation (Case, 1978; Thonney *et al.*, 1976).

2. Currently a practical accurate method for size determination is lacking. There is a much higher precision required to estimate genetic size at the intra-specific level than needed for inter-specific purposes (Fitzhugh and Taylor, 1971; Taylor, 1985).

If differences in genetic size decrease, variation due to size will become less important relative to typical non-size variation. Generally inter-specific variation in size is of a much larger magnitude than intra-specific variation. The precision in determination of genetic size therefore is more important in intra-specific comparisons, because here determination errors are proportionally much larger.

Intra-specific scaling

The best documented and most outstanding deviation of intra-specific scaling from inter-specific scaling patterns is gestation length, which is virtually constant among breeds and strains (Taylor 1987a). This constancy distorts to some extent the standard relationship between metabolic age and degree of maturity of the body weight, if we take birth as a reference point for comparison. In a discussion on intra-specific scaling, Taylor (1987b) concluded that size scaling provides the best method for breed evaluation, although degree of maturity in body weight should be preferred to metabolic age as basis for comparison. In general it is believed in this thesis that the degree of maturity in terms of proportions of A is a much more stable basis for comparison than metabolic age, at all levels of scaling. Numerous (environmental) factors may affect the growth rate of an individual and hence metabolic age at a given

developmental stage, whereas it is expected that body mass at such a stage is far less changed by these factors. This means that in the second scaling rule, degree of maturity of body weight should be preferred over metabolic age, as a reference measure for development.

The required precision in determination of genetic size makes it difficult to assess the validity of reported intra-specific relationships that deviate from the expected inter-specific patterns. For instance in their literature review of intra-specific relations of fasting metabolism, Thonney *et al.* (1976) report scaling coefficients for human adults that range between 0.33 and 0.63. It is generally known that weight variation in human adults to a considerable degree can be attributed to body fat (Forbes *et al.*, 1986), and thus represents a mixture of variation in genetic size and physiological status. It may therefore be questioned whether such low scaling coefficients can really be accepted as evidence for deviation from inter-specific patterns. What is essentially needed for evaluation of intra-specific scaling is an approach which enables a sharp distinction between developmental and nutritional variation on one hand and genetic size on the other. In the following sections aspects of genetic size determination will be discussed more extensively.

Determination of genetic size

Body size is the result of increase in cell number and cell size. After conception, the multiplication of cells (hyperplasia) in mammal species primarily takes place during the embryonic stages of development. Subsequent growth is dominated by enlargement of cell size (hypertrophy), except for adipose tissue, which probably also shows hyperplasia during postnatal growth (Hood and Thornton, 1979). Cell sizes of adult animals hardly differ between differently sized species (Berril, 1955). Accordingly genetic size is a reflection of the initial embryonic stages of growth. Embryonic differences between the small Polish rabbits and the much larger Flemish giant provide a clear example of this early expression of genetic size (Berril, 1955). After two days, the embryo of the giant breed has already about 1.6 times more cells. One may therefore say that genetic size is primarily determined by cell number, rather than cell size.

Cell numbers, however, do not offer a practical basis for genetic size determination as they are virtually uncountable in mammals after the initial embryonic stages. If we want to introduce the scaling theory in common animal husbandry and breeding practice we should look for a relatively simple measure. For a practical ideal measure of genetic size we may formulate the following five conditions:

1. The measure should explain as much as possible inter-specific and intra-specific variation of cumulative, rate and time variables at any stage of development.
2. It should correspond to a clearly identifiable, equal stage of development.
3. It should be independent of the animal's nutritional and environmental history.
4. It should be determined at a developmental stage that lies within the normal weight range of farm animals, preferably as early as possible.
5. It should be a simple external measurement, easy to measure *in vivo*.

So far most determination methods of genetic size are based on adult weight, normally denoted by the symbol A. In favour of this choice, Taylor (1985) argued that full maturity is the only period during development when body size is potentially in an unchanging state, and that it is more stable than any other measure. Determination based on adult weight, however, is not that straightforward as it might seem, in particular not at the individual level, as demonstrated by a number of breed evaluation experiments based on size scaling. Even if restricted to ruminant species only, we may observe a variety of determination methods and related practical and conceptual problems. The most frequently used methods are discussed below.

Maximum weight

In most experiments adult weight is implicitly assumed to be the maximum weight an animal is able to attain. Unfortunately there is a long and laborious way to go before ruminants will reach this level. Therefore A is often derived from extrapolating weight relationships toward their asymptotic level, thus restricting recording periods and efforts. Usually A is estimated from weight-age relations, applying one of the many growth models available in literature. In the

approach of Parks (1982), A is derived from the asymptote of the Spillman function, regressing weight on cumulative food intake (Thompson and Parks, 1983; Thompson *et al.*, 1985a). The accuracy of these approaches depends both on the model used and the actually observed weight range.

Blaxter *et al.* (1982) demonstrated that if continuously *ad lib* fed sheep eventually neared maximum weight, they were far beyond the normal weight range of breeding animals. These animals became extremely fat, reaching fat levels of 50% and more in their empty body weight. One may therefore question whether these final levels are not expressing their propensity to fatten, rather than reflecting a size factor that is related to the whole growth curve. Similarly, in non-ruminant species like pigs (Walstra, 1980) and poultry (Prescott and Wathes, 1985) maximum weight levels are far out of range of normal farm animals, and animals become very fat.

Blaxter *et al.* (1982) also raised the question, whether maximum weight of *ad lib* fed animals could be modified by nutritional factors, which would be very undesirable for a measure of genetic size. In their own experiment they found no effect of energy density of the diet on maximum weight, but they commented that such an effect is not unlikely if a larger contrast in diet quality would have been imposed. In his theory of growth Parks (1982) maintained that both mature weight and composition at maturity may vary with environmental factors such as the energy and protein content of the ration, but indicated no experimental support for this hypothesis. Experimental data on this topic, other than from Blaxter's study, appear to be very scarce, and as far as known, not available for ruminants. The issue is of importance for understanding how growth and intake are regulated in reaching an equilibrium weight, and requires further experimental investigation.

Fat-adjusted mature weight

In an attempt to overcome the conceptual and practical problems related to maximum weight some workers opted for excluding the final fat growth from the determination of genetic size. In principle this approach aims at identifying a physiologically equal stage of maturation before all tissues, in particular fat, are fully mature.

Especially in studies on body composition this approach has been adopted. In such studies extrapolation toward maximum weight is not possible because the actual composition of 'full grown' animals is required as a reference basis for description of growth. In a study on composition of Merino strains, Butterfield *et al.* (1983) regarded rams as mature, when weekly liveweight gains had become 'minimal' and where muscle plus bone weight had 'apparently' ceased to increase. Doney *et al.* (1988) defined maturity as the stage at which further muscle growth was expected to be minimal. They considered lambs over the age of 1 year, that remained in equilibrium for at least 4 weeks, to be mature. It is not clear how this criterion relates to minimal muscle growth. Cessation of growth for one month followed by long periods of growth is a quite normal phenomenon in long term growth trials. Thompson *et al.* (1985b) accepted an animal as mature when it had reached at least 0.85 of its asymptote and the average weekly growth was zero for at least 10 weeks.

The problem these studies have in common, is that their concept of maturity requires knowledge of changes in composition of body gain, preferably *in vivo* during growth. This cannot be easily derived from the pattern of growth and certainly not from occasional fluctuations in growth rate as some of them do. More or less in line with the approach of excluding final fat growth, Taylor (1985) proposed to adjust mature weight to a chemical body fat content of 20%. In addition, he defined mature body weight, as the weight of a normally grown animal, that is skeletally mature, normally active and is maintained at an equilibrium weight on a standard diet, in a thermoneutral, disease-free environment. Kyriazakis and Emmans (1992) based their determination of size on final ash weight only. Again the same practical problem applies. As long as no practical and accurate *in vivo* methods for determination of body composition are developed, determination depends on laborious slaughtering methods. The desired individual *in vivo* assessment of genetic size, based on body composition characteristics, therefore is waiting for alternative methods.

Dam weight

McClelland *et al.* (1976) examined breed differences in body composition of 4 sheep breeds by slaughtering at equal degrees of maturity. To do so they had to determine the genetic size of the experimental animals before the trial, in

order to define slaughter points in advance. For this purpose they utilized the weight of the dam (d) and the least squares mean weight of ewes for each breed (D), that were kept in the same nutritional environment. The mature weight (M) of a female lamb was estimated as $M = 0.35d + 0.65D$ on 'the assumption, that the heritability of mature ewe weight was about 0.7 and the dam-offspring regression was therefore about 0.35'. For male lambs, M was multiplied by 1.30, which was assumed to be the sex ratio for mature weight. Thonney *et al.* (1987) followed the same procedure in their series of papers, where they compared feed intake and body compositions of males and females of sheep and goat breeds, but only used mean breed weights. They remarked that the pasture weights of the dams were far below weights attained by animals on their experimental diet of which some were 1.3 times heavier.

In principle this method offers a fairly accurate indication of how breeds rank in genetic size, on the condition that reference dams are raised and bred in exactly the same (nutritional) environment. In normal animal husbandry practice this is usually not the case. The method can therefore only be applied in carefully designed breed evaluation experiments with adequate numbers of dams per breed. The value of these calculated sizes is restricted to establishing relative size differences and cannot be compared to values from other experiments with different environmental conditions.

A stronger experimental basis is needed for using the multiplication factor of 1.3 as the sex ratio. The ratio might differ between breeds. Thompson *et al.* (1985a) found in Merino's strains, selected for low and high growth rate, larger sex ratios (1.34-1.54), which differed between strains. The theoretical basis of the method proposed by McClelland *et al.* (1976) is not a very solid one. The assumed heritability is rather tentative and needs further verification. Combining this tentative element with the uncertainty of the sex ratio, individual estimates become especially unreliable for male animals.

Prospects for improvement of size determination

Starting from the concept of 'adult' or 'mature' weight as a basis for size determination, three different approaches could be distinguished: maximum weight, fat-adjusted weight and dam weight. The first two rely on individual

performance and the latter on maternal information. It is believed here that the best and most direct approach of determining individual genetic size has to be the animal's own performance, and not those of related animals. The precision of dam-based genetic size is not only dependent on the accuracy of determination of dam weight, which can be quite troublesome given the many fluctuation in weight throughout the breeding season, but also on the accuracy of relationships between size of parents and offspring. Nevertheless dam weights might prove to be useful in cases where in an early stage of growth individual information on genetic size is required. However, it is not seen here as a solid basis for further development of size determination.

Both maximum weight and fat-adjusted weight are based on individual performance. None of them matched all the conditions, as outlined before, for a simple measure of genetic size. Maximum weight is not easily measured, because a laborious and time-consuming method is required for determination. The trait cannot be precisely determined in normal breeding animals that have a much lower equilibrium level. It is not sure whether nutritional factors affect final weight. Nevertheless maximum weight is a trait that can be estimated without sacrificing the animal and refers to a clearly definable stage of growth.

The attractive element of fat-adjusted weight lies in leaving adult weight as the single basis for genetic size. Theoretically there is no reason why immature stages are not acceptable as a basis for genetic size determination. The effectiveness of the scaling theory in animal production practice would be significantly improved if genetic size can be estimated at an early growth stage. It is questionable, however, whether fat-adjusted weight is a suitable measure. Fat-adjusted weight has the main disadvantage that it relies on changes in body composition that are difficult to measure *in vivo*. Moreover, the percentage of body fat *per se* has not a direct functional significance in the animal's ontogeny, except that the level of body fat is increasing as animals mature. Domesticated breeds are said to be in general intrinsically fatter than feral animals (Blaxter, 1989), and comparing these animals on basis of a fixed fat percentage would therefore lead to unjustified conclusions.

The problems related to fixed fat percentages can be partially circumvented by trying to identify possible phases in fat deposition that are linked to functional stages of development. The body weight at the onset of a particular developmental stage could then be used as a measure of size, as it represents an equivalent stage of development. Alternatively we also might consider functional development characteristics of other body components as a basis for size determination. Especially those body components are of interest that show phasic development patterns. Body weight at transition from one phase to another could serve as a genetic size measure. To select such promising alternatives more detailed knowledge is required of phasic growth patterns. Both growth characteristics of components expressed on basis of age, as growth relative to other parts or total body weight might provide useful reference marks for size determination.

In conclusion, knowledge of scaling relationships is of unquestionable importance for animal production. They provide the biological basis for understanding of a substantial part of variation in growth and other forms of production. In particular the concepts of the genetic size scaling theory of Taylor are of considerable interest for genotype evaluation. The major constraint in using this theory in animal production, however, is the lack of a suitable measure for genetic size. Current determination methods of size are mainly based on adult weight. It is concluded here that, instead of adult weight, a more promising approach for measuring genetic size might be to look for early characteristic changes in growth of body components that are linked to functional stages in development.

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CHAPTER 2

EFFECTS OF BREED AND FEED QUALITY ON PARAMETERS OF AN INTEGRATED FEED INTAKE AND GROWTH MODEL OF TWO GOAT BREEDS

ABSTRACT

An integrated feed intake and growth model is presented, based on the relationships between respectively weight (W) and cumulative feed intake (F), and W and age (t). The models were used to analyze effects of breed and feed quality on individual intake and growth data of two goat breeds between weaning and full maturity. Two breeds were compared: 10 Saanen goats (group S) and 8 West African Dwarf (WAD) goats (group DH), both fed ad libitum pellet H (10.7 MJ ME/kg DM). Effects of feed quality were examined by comparing DH to another group of 10 WAD goats (DL), fed pellet L ad libitum (7.5 MJ ME/kg DM).

Feed quality did not affect the asymptotic weight (A) of the WAD goats (DH, 48.1 kg; DL, 52.1 kg). The feed intake curve against u (= W/A) of DH, was more convex in approaching adult intake than the curve of DL. The feed efficiency parameter (AB) was lower for the L feed (DH, 0.262; DL, 0.172). The maturation rate (du/dt) of DL was lower than the rate of DH. There was a strong breed effect on A (S, 109.6 kg). The shape of the size-scaled feed intake curve was similar for S and DH, but its magnitude was at comparable u higher for S. At u = 1 the estimated scaled intake of S was 1.18 times the intake of DH. Group S converted their feed more efficiently than DH (AB for S: 0.291). There was no breed effect on du/dt. Size-scaling of the time component dt by $A^{0.27}$ in maturation rate du/dt, resulted in a higher scaled maturation rate for S. In this specific case, growth traits of both breeds can be better compared on basis of normal age than scaled age.

EFFECTS OF BREED AND FEED QUALITY ON PARAMETERS OF AN INTEGRATED FEED INTAKE AND GROWTH MODEL OF TWO GOAT BREEDS

INTRODUCTION

Comparisons of feeding and growth traits are normally based on performance at equal age, equal weight or equal stage of development. If genotypes of different genetic size are studied, however, equal age or weight levels do not represent necessarily similar stages of development and provide no correct basis for assessment of genotypical effects. In such comparative studies, the non-specific effects of varying size present another complicating factor. Here the concepts of genetic size and degree of maturity from the genetic size-scaling theory (Taylor, 1980) may offer a valuable basis for evaluation.

In the genetic size-scaling theory two main sources of variance of traits are distinguished: variance due to genetic size and specific size-independent variance. The size component of variance can be removed by scaling all input, output and time variables by the genetic size, defined on basis of the adult weight (Taylor, 1980). The degree of maturity can be expressed in terms of the scaled weight or age. To assess specific genotype effects, scaled traits have to be evaluated at equal degree of maturity.

Two different approaches can be distinguished for analysis of feeding and growth traits at equal degree of maturity. Average levels might be studied at a number of different degrees of maturity (Thonney *et al.*,1987). Another option is to model the relations between input, output and time variables over a wide range of degree of maturity. The parameters of such models should enable assessment of the genotype and treatment effects at a similar degree of maturity. The integrated feed intake and growth model published by Parks (1982) is an example of the latter approach.

It is preferred that integrated feed intake and growth models contain parameters which allow separation of size and size-independent effects. Their parameters should be interpretable in relation to the scaled feed intake and growth variables. The main advantage of the model approach is a more fundamental

understanding of genotypical and environmental effects and their interactions. Studies based on a model approach however are scarce, probably because both intake and growth data have to be collected from an extended part of the growth curve to obtain reliable parameter estimates. A lack of suitable models also might have played a role here.

The first objective of this study was to construct a set of models to describe the relations between feed intake, weight and age. The selected models should contain parameters which can be interpreted meaningfully in relation to the (scaled) feeding and growth traits. The second objective was to apply these models to data of individual animals collected in an intake trial with two goat breeds. The effects of breed, separated in genetic size and specific breed effects, and feed quality on the individual parameters were assessed.

AN INTEGRATED FEED INTAKE AND GROWTH MODEL

The main variables, involved in the input and output relations in growth, are cumulative feed intake (F), weight (W) and age (t) (Parks, 1982). Three basic relationships can be distinguished: F-W, W-t, F-t (Chapter 1, Figure 1). In an integrated feed intake and growth model two relationships have to be defined, from which the third relationship and all other derivatives follow. The proposed set of models in this study is based on two basic models describing the relations between F and W, and W and t. Because the scaling procedures for time variables in breed comparisons are not fully established (Taylor, 1987), variable t and the time component in rate variables are not *a priori* scaled by size in this set of models. In addition to the two basic models, all relationships between degree of maturity and rate variables, and degree of maturity and efficiency of feed use will be given in the next paragraph.

First the relation between W and F is described by model (1) (Parks, 1982):

$$W = A\cdot[(1-u0)\cdot(1-e^{(-AB\cdot F/A)})+u0]+\underline{e} \qquad (1)$$

with the variables:

W = liveweight (kg)
F = cumulative DOMI (,,)

$\underline{e}$ = random error (,,)

and the parameters:

A = asymptote of W (kg)
u0 = W/A at F=0
AB = measure of feed efficiency

The degree of maturity (u) can be expressed as W/A. An important implication of (1) is that the feed efficiency (dW/dF) in relation to u is exclusively determined by AB:

$$dW/dF = AB \cdot (1-u) \quad (2)$$

AB can be regarded as a parameter that summarizes the overall feed efficiency performance at given u, irrespective of A.

In the second step, for each animal the relation between W and t is described by a two-parameter model (3), with estimates of A and u0 from (1) as fixed parameters:

$$W = A \cdot [(1-u0) \cdot (1-e^{-k \cdot t})^{(1/n)} + u0] + \underline{e} \quad (3)$$

with the variables:

W = weight at age t (kg)
t = age (t=0 at F=0) (d)
$\underline{e}$ = random error (kg)

and the parameters:

k = maturation rate parameter (see below) (d^{-1})
n = coefficient determining shape of curve
A = fixed parameter from (1) (kg)
u0 = fixed parameter from (1) (fraction)

From model (3), it follows that growth rate (dW/dt) can be expressed as a function of u:

$$dW/dt = A \cdot k \cdot (1/n) \cdot (u-u0)^{(1-n)} \cdot [(1-u0)^n - (u-u0)^n]. \quad (4)$$

Growth rate can also be expressed relative to A, which is called here the maturation rate du/dt (=(dW/dt)/A), with unit d^{-1}. The maturation rate at given u is determined by k, n and u0. In Figure 1, du/dt as a function of u is shown for varying values of n. It is demonstrated that for $n \neq 1$, du/dt nears asymptotically the line $k \cdot [(1-u0)-(u-u0)]$ belonging to n=1. From Figure 1 it can

be seen that at increasing u, k is the principal parameter determining maturation rate.

The relation between feed intake (dF/dt) and u can be derived from (2) and (4), since dF/dt = (dW/dt)/(dW/dF):

$$dF/dt = A \cdot k \cdot AB^{-1} \cdot (1/n) \cdot (u-u0)^{(1-n)} \cdot [(1-u0)^n - (u-u0)^n]/(1-u) \qquad (5)$$

If u nears 1, adult feed intake can be estimated as $A \cdot k \cdot AB^{-1}$. Parameter n characterizes both the shape of the weight curve (3) and the feed intake curve (5). If n increases from 0 to 1, the feed intake curve is becoming more convex in its approach to adult intake, and for n = 1, feed intake is constant irrespective of u.

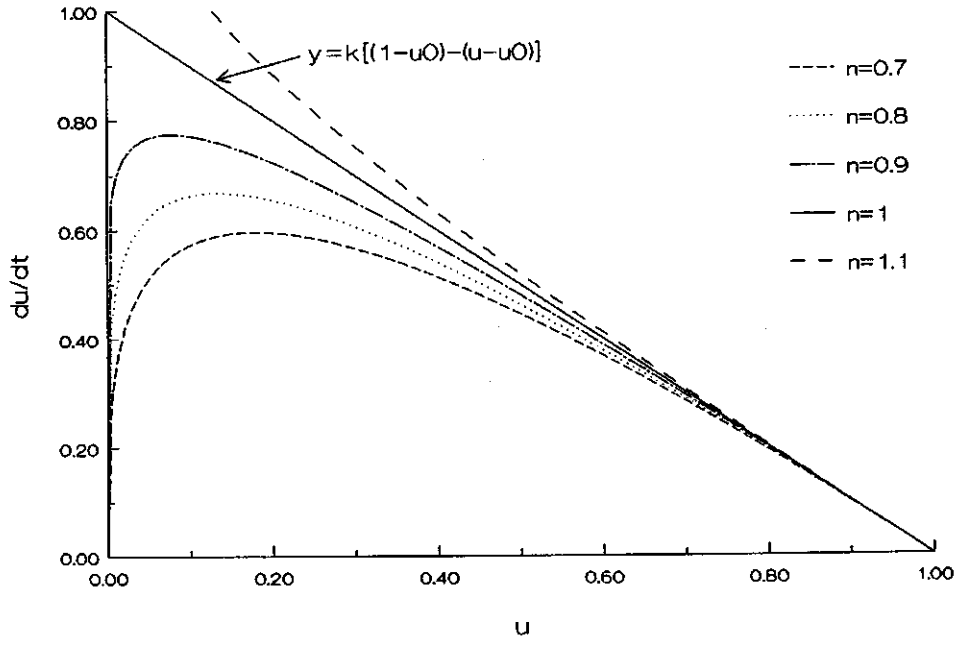

FIGURE 1. *The relationship between maturation rate (du/dt) and u, based on model (4) (see text), for varying values of parameter n, and k = 1 and u0 = 0.*

MATERIAL AND METHODS OF THE INTAKE TRIAL

Experimental design

Data for this study were derived from the results of a main experiment with castrated male goats from the Saanen breed, a large sized European dairy breed, and the West African Dwarfgoat breed (WAD breed), one of the smallest breeds. Growth and individual intake were recorded and whole body composition determined according to a cross-sectional design. This study focuses on the growth and feed intake section.

The experiment consisted of two parts starting at different times. In the first part, goats were born in February and March 1987, and the recording of their feed intake commenced in August 1987. One group of the WAD goats (DH1) and all the Saanen goats (S) were fed *ad libitum* pelleted concentrates (feed H). The remainder group of WAD goats (DL1) received *ad libitum* less digestible, pelleted alfalfa (feed L). Both WAD treatments were repeated in the second part (groups DH2 and DL2). WAD goats in this part were born in September and October 1987, and their feed intake recording started in May 1988.

At consecutive age intervals, from birth to a maximum age of nearly three years old, randomly selected animals within each group, were slaughtered to determine body composition. This study describes results of animals for which feed intake was measured during a period of at least 14 up to a maximum of 30 months. Table 1 shows numbers used in the analysis and the length of the recording periods.

Management

The WAD kids stemmed from a WAD herd, kept for experimental purposes, and the Saanen kids from a dairy herd. Both herds and experimental animals were housed at a goat unit of the Wageningen Agricultural University. The stable was heated during winter to maintain thermoneutrality. An artificial lighting regime was imposed of 12 h light and 12 h darkness to avoid seasonal effects of day length.

TABLE 1. *Number of animals used in the analysis in each group, and its distribution over three intervals of total number of recorded weeks*

Group	61-80 weeks	81-100 weeks	101-130 weeks
S	2	1	8
DH1	1		3
DH2	4		
DL1	2		5
DL2	2	2	

The WAD goats were allotted randomly to the treatment groups. Kids from S, DH1 and DL1 were reared artificially on a milk replacer fed *ad libitum*, and had free access to hay and concentrates. Kids of DH2 and DL2 were raised with their dam. All kids were weaned at nine weeks. Both breeds were accustomed to the treatments by reducing gradually the hay and concentrate proportion in the ration. From an age of 13 weeks on, only experimental feed was offered. Most animals in DH2 and DL2 showed a low intake and poor performance during a prolonged period after weaning. Here the pre-treatment concentrates and hay were offered until an age of 20 weeks.

After weaning, groups of four animals each were placed in 4x4 m pens, embedded with sawdust. The pens were equipped with electronic Calan gate-feeders, adapted for goats, to measure individual feed intake. After a training period, intake recording started at a mean age of six months in the first group and in the second at a mean age of 7.5 months. Feed, fresh water and salt licks were available all day. Feed was regularly supplemented to maintain at least 1.5 kg in the troughs. Each week full liveweight and weekly feed intake were recorded.

At regular intervals, all animals were treated against worms and ectoparasites and had their hooves trimmed. Digestive disorders occurred one or two times in most animals at the H feed in their first year, from which they normally quickly recovered. Three animals in S and three in DH suffered of urinary retention problems due to urinary calculi; their data were not used in this

analysis. One animal, showing signs of chronic arthritis, and one with skin problems, both retarded in growth, were also excluded from the analysis.

Feeds and digestion trials

The H feed was renewed four times during the experiment. Each batch (I to IV) had the same composition of ingredients. Also four batches of the L feed (I to IV) were fed. Composition and mean concentrations of dry matter (DM), organic matter (OM) and crude protein (CP) are in Table 2. Four digestion trials were conducted to quantify effects of feed, batch, breed and intake on OM digestibility (dOM).

TABLE 2. *Composition of the experimental diets (g kg^{-1}), and the mean dry matter (DM), organic matter (OM) and crude protein (CP) concentrations (g kg^{-1}) averaged over the batches of feeds H and L, with the sample s.d. of the batches*

Component	Feed H	Feed L
Alfalfa	323	1000
Cassava meal	225	
Soybean meal (extracted)	188	
Maize	113	
Maize glutenfeed	77	
Molasses	53	
Calcium carbonate	11	
Salt	6	
Mineral premix	4	
DM	898 ± 13	911 ± 4
OM in DM	895 ± 5	870 ± 8
CP in DM	182 ± 2	143 ± 7

Four castrated male Saanen goats and four female WAD goats were used to test the H feed, and another four female WAD goats for the L feed. They were of the same age as S, DH1 and DL1, and were fed their test feed *ad libitum* between the trials. In each trial, animals were consecutively offered two feeding

levels, one near maintenance and one *ad libitum*. The trials started with an adaptation period of 14 d in metabolism cages after which in a seven-days period dOM was measured. Intake levels were then changed over and after two weeks dOM was measured again during periods of seven days. During these periods offered feed, collected feed refusals and faeces were recorded and subsampled for DM and ash determination.

The results from the digestion trials were analyzed by the following statistical model for each feed separately:

$$y_{ijk} = \mu + a_i + c_j + (a*c)_{ij} + b_{ij}(DMI/MW)_{ijk} + \underline{e}_{ijk}$$

where y_{ijk} is dOM, μ is the overall mean, a_i is the effect of breed (only in the H feed), c_j is the effect of batch j, b_{ij} is the regression coefficient within breed j and batch j, and DMI/MW represents the covariate DM-intake per kg metabolic weight (g d^{-1} $kg^{-0.75}$).

No effect of breed was detected on dOM of the H feed nor any interaction between breed and batch or regression coefficient b. In both feeds, effects of batch (H:$P<0.01$, L:$P<0.001$) and of the covariate DMI/MW (H:$P<0.01$, L:$P<0.001$) were significant, but there were no interactions between batch and the covariate DMI/MW. The resulting regression equations for both feeds are summarized in Table 3. These equations were used to calculate intake of digestible organic matter (DOMI). The estimated concentration of metabolizable energy (ME) in the DM is also given in Table 3, based on the assumption that 1 g DOMI is equivalent to 15.8 kJ ME (NRC, 1981).

Analysis of model parameters

For each goat, parameters were estimated by fitting model (1) to cumulative DOMI and W, followed by model (3) using the DUD nonlinear regression procedure (PROC NLIN; SAS, 1985). Results from DH1 and DH2, and from DL1 and DL2 were combined into two treatment groups (DH and DL respectively). Size and significance of two linear contrasts BR and F, representing effect of breed and feed, were examined for each parameter (PROC GLM; SAS, 1985). Contrast BR was defined as the linear combination of treatment effects S-DH,

and contrast F as ½S + ½DH-DL; F-tests were used to test whether contrasts were significantly different from zero. Two additional scaled parameters were also included in the analysis; f_{max} (= $A \cdot k \cdot AB^{-1}$, in g d $kg^{-0.73}$) representing the adult intake scaled by $A^{0.73}$, and $k/A^{-0.27}$ representing the maturation rate, but now including a scaled time component. The unit of the latter parameter can be expressed as (metabolic day)$^{-1}$, where metabolic day is defined by Taylor (1980) as days/$A^{0.27}$.

Correlation and partial correlation coefficients between the parameters were determined within each group. Scaled mean weight and feed intake curves were constructed in each group, by calculating and averaging individual points at 10 different values of t or u, using the equations (3) and (5). The chosen values of t and u represented the range covered in this experiment.

TABLE 3. *Regression of digestibility of organic matter on dry matter intake for feeds H and L, with the regression coefficients (b), intercepts for each feed batch, standard errors (s.e.) and residual s.d., and estimated mean concentrations of metabolisable energy (ME) in the dry matter (DM) for H and L*

	Feed H		Feed L	
	estimate	s.e.	estimate	s.e.
intercept:				
Batch I	0.770	0.014	0.575	0.023
Batch II	0.798	0.011	0.657	0.022
Batch III	0.796	0.011	0.625	0.020
Batch IV	0.781	0.011	0.616	0.017
b	-0.0889	0.0257	-0.1514	0.0319
residual s.d.	1.90		1.76	
MJ ME/kg DM	10.66		7.46	

RESULTS OF THE INTAKE TRIAL

Fitting of models

Fitting of model (1) and (3) resulted in stable estimates for all animals, except two animals (one in S, one in DL). The latter two produced aberrant estimates of A and AB with large asymptotic standard errors, and their results were excluded from the analysis. Asymptotic correlations between estimates of A and AB in (1) and between k and n in (3) were high, in general being larger than 0.90. The mean residual standard deviation (r.s.d.) in (1) was of similar size in DH and DL and about four times higher in S (Table 4). In some animals these residuals showed a slightly oscillating pattern. No consistent pattern could be detected however, nor any indication of seasonality. Fitting of model (3) led to a somewhat higher r.s.d. in all groups.

Parameter means

Group means of parameters from (1) and (3) are in Table 4. The means of A illustrate the larger size of the Saanen goats, and indicate similar levels for both feeds in the WAD goats. The feed efficiency parameter AB was lower for the L feed; the mean AB of DL amounted 59% of the mean of S and 66% of the mean of DH. The lower growth rates of DL during the preceding adaptation period of the intake trial, resulted in lower values of u0 compared to DH and S. Mean ages ($\pm$s.d.) at u0 were 171 $\pm$ 8, 195 $\pm$ 43, 203 $\pm$ 25 days for S, DH and DL respectively. Means of parameters k and n were of comparable size in S and DH, and both at a lower level in DL. Means of f_{max} indicated a 20% higher level in S compared to the combined means of DH and DL. Parameter $k/A^{-0.27}$ showed a relatively much larger difference between the breeds than its unscaled form.

Contrasts

The size and significance level of the orthogonal contrasts BR and F are presented in Table 5. Although A and u0 did not meet the condition of required homogeneity of variance, an F-test was applied here to test whether they were significantly different from zero. Contrast BR showed a strong effect for parameter A, and was significant for AB, f_{max}, and $k/A^{-0.27}$, but not for u0, k and n. Contrast F was significant for all parameters. The inclusion of both

breeds in contrast F affected contrasts of parameters that were subject to breed effects. The parameters k, n and u0 were not affected by breed, and here the size of contrast F can be fully attributed to feed.

TABLE 4. *Parameter estimates from model (1) and (3) (see text) for groups S, DH, DL: mean residual s.d. and group means of parameters A (kg), AB, u0, k (d^{-1}), n, f_{max} ($g\ d^{-1}\ kg^{-0.73}$) and $k/A^{-.27}$ (metabolic day)$^{-1}$ with the sample s.d. in each group*

Parameter		S (n = 10)	DH (n = 8)	DL (n = 10)
Residual s.d. (1)		1.839	0.416	0.511
Residual s.d. (3)		2.099	0.465	0.570
A	mean	109.6	48.1	52.1
	s.d.	10.2	3.2	12.5
AB	mean	0.291	0.262	0.172
	s.d.	0.038	0.024	0.022
u0	mean	0.289	0.284	0.227
	s.d.	0.022	0.052	0.010
k (x100)	mean	0.256	0.242	0.153
	s.d.	0.055	0.040	0.045
n	mean	0.909	0.933	0.768
	s.d.	0.080	0.072	0.081
f_{max}	mean	30.9	26.1	25.3
	s.d.	2.62	2.20	4.05
$k/A^{-.27}$(x100)	mean	0.906	0.688	0.438
	s.d.	0.182	0.113	0.108

Correlations

Correlation coefficients (r), calculated within each group, are in Table 6. In all groups AB and k were significantly positively correlated. The occurrence of other significant correlations were limited to single groups. Partial correlation coefficients $r_{AB\text{-}k.An}$ were calculated to test whether the strong relationship

between AB and k was affected by the level of A and n. In S and DH values of $r_{AB\text{-}k.An}$ were almost equal to r, being 0.97 and 0.95. In DL $r_{AB\text{-}k.An}$ was 0.96, which is at a higher level than r.

TABLE 5. *Estimates and significance of contrasts BR and F (see text) for parameters A, AB, k,n and f_{max}, $k/A^{-0.27}$ with the residual s.d. of the used model*

Parameter	Contrast[1]				Residual s.d.
	BR		F		
	est.	sign.[2]	est.	sign.[2]	
A	61.43	**	26.79	**	9.80
AB	0.029	*	0.105	**	0.0295
u0	0.005	ns	0.059	**	0.0360
k (x100)	0.014	ns	0.096	**	0.0475
n	-0.023	ns	0.153	**	0.0779
f_{max}	4.77	**	3.22	*	3.12
$k/A^{0.27}$ (x100)	0.218	**	0.359	**	0.1401

[1] BR = S-DH ; F = ½S + ½DH-DL
[2] * $P<0.05$; ** $P<0.01$ (throughout this thesis)

Weight and feed intake curves

In Figure 2 the average development of u against age (since conception) was constructed for each group. The first two points were not computed but were the actual recorded values of u at birth and at weaning. Calculated values of u, representing the recording period, did all show higher values in S compared to those of DH. The shape of the u curve against the (unscaled) age of animals fed the H feed was remarkably similar in both breeds. The effect of feed quality was clearly illustrated by the different shape of the u curve of DL.

In Figure 3 the average feed intake curve, scaled by $A^{0.73}$, against u was constructed for each group. The equal levels of n for DH and S were reflected by similar curve shapes, but the curve of S showed a permanent higher level in

this range of u. The shape of the curve for DL differed substantially from those of S and DH as indicated by the feed effect on parameter n. The feed intake curve of DL started at a lower level and finally approached the curve of DH at increasing degrees of maturity.

TABLE 6 *Size and significance of correlations between parameters A, AB, K, N, U0 within groups S, DH, DL. Correlations of DH are above the diagonal of the upper block, those of S are below the diagonal*

	S\DH				
	A	AB	K	N	U0
A		-0.25	-0.17	-0.42	-0.18
AB	-0.75**		0.95**	0.19	0.92**
K	-0.63	0.98**		0.17	0.83*
N	-0.11	-0.33	-0.47		0.45
U0	0.03	-0.20	-0.31	0.86**	
	DL				
	A	AB	K	N	U0
AB	-0.24				
K	-0.76*	0.72*			
N	0.50	-0.11	-0.64*		
U0	-0.60	0.57	0.62	0.10	

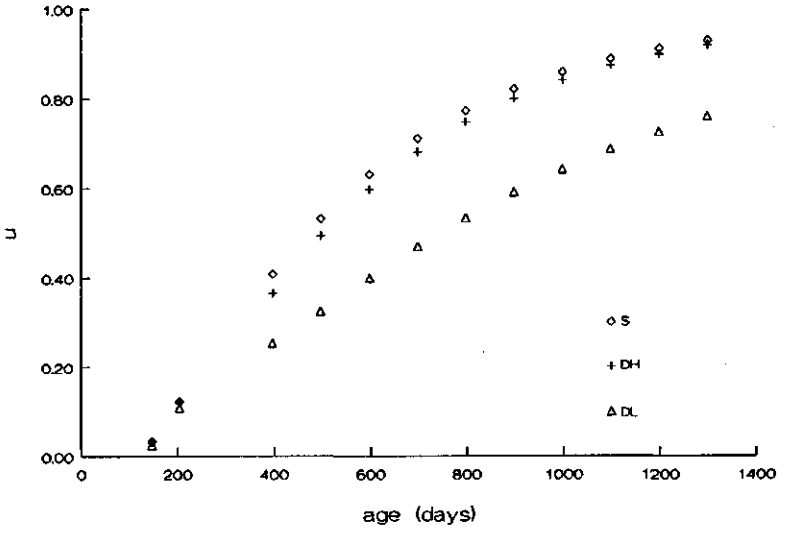

FIGURE 2. *The development of the mean u against age from conception (days) for groups S, DH and DL. The first u-value at birth and the second at weaning are means of recorded weights scaled by A. The other values are based on the model estimates of the individual animals.*

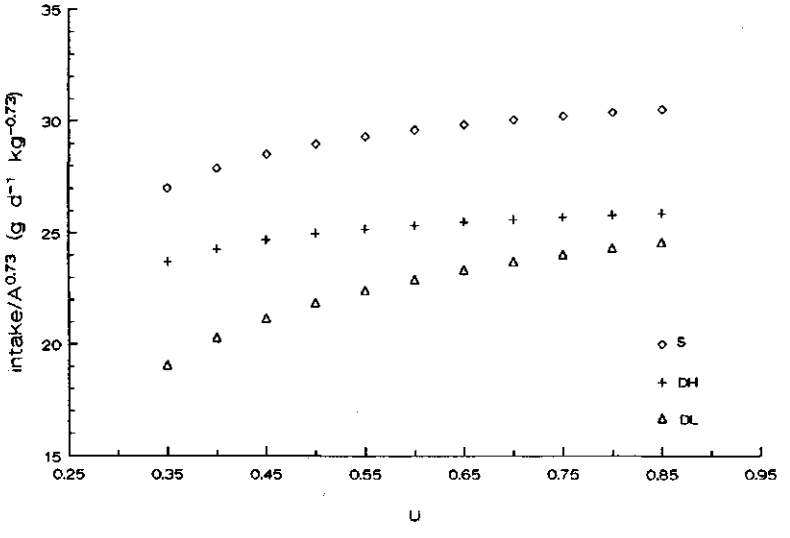

FIGURE 3. *The development of the mean feed intake (g d^{-1} $kg^{-0.73}$), scaled by $A^{0.73}$, against u, for groups S, DH and DL. Feed intake values are based on the means of the model estimates of the individual animals.*

DISCUSSION

Choice of models

In a preliminary analysis of the presented data, the set of models described by Parks (1982) was used, to allow an analysis compatible with the objectives of this study. Here unrealistic estimates were derived from the feed intake-age model for animals with the relatively shorter recording periods. This could be explained by the high sensitivity of parameters to random deviation in intake in the final part of the recorded data. In the study of Parks some results showed similar problems for the feed intake-age model. For example, the estimated asymptotic feed intake for Jersey cattle (p. 57/58) suggested a very high intake level of 86 g TDN $kg^{-0.75}$ at full maturity.

In this study, the analysis started from the approach of Parks, using the same model for the W-F relation, but described the age-linked relations differently. Age was used in model (3) to fit directly variable W instead of feed intake. Here parameters were relatively less sensitive to random deviation at the end of recording, due to the cumulative character of W. Parameters A, AB and k from the approach in this study can be easily compared with the parameters A, AB and the parameter for adult intake from the approach of Parks, because (A·k) = (adult intake·AB).

Asymptotic weight (A)

The difference of 61.4 kg between the means of A for S and DH illustrated the different breed size. The considerably lower nutrient density of the L pellets did not result in a smaller A in DL (Table 4). Blaxter *et al.* (1982) neither could demonstrate an effect of quality of pelleted feeds on A of crossbred sheep. Diet effects on A in a wider range of diet qualities, including low-quality roughages, might still be possible, but conclusive evidence from the literature is not available so far. The absence in this trial of diet effects on A underlines the appropriateness of asymptotic weight as a measure for genetic size.

Feed efficiency (AB)

Parameter AB was higher for the Saanen breed (Table 5). Small strain effects on AB were also shown by Thompson *et al.* (1985) between three strains of

Merino rams and ewes. Variations in AB of breeds, kept in comparable nutritional environments, can be attributed to various factors, which are involved in the conversion of feed into weight. Here the efficiency factors for gain and maintenance play an important role as does body composition. The type of data presented here, however, allow no further identification of breed effects on these underlying factors.

In this trial, AB was expressed on basis of cumulative IDOM to correct for different nutrient densities in the DM of both feeds. Even on this corrected basis, AB was clearly lower for DL, being 66% of the value estimated for DH. This could be related to the lower metabolizability (q) value of L. Low q values are associated in ruminants with low efficiencies in the conversion of ME into energy for gain (ARC, 1980). Low q values result also in low intake levels above maintenance (ARC, 1980), as shown in this trial for DL when compared to DH (Figure 3). Lower intake levels lead to proportionally higher maintenance costs and therefore lower feed efficiencies.

In order to compare own goat estimates with estimates of sheep, values of AB from literature based on fresh feed, were converted to values based on the digestible OM (DOM) concentration of the feed. Converted values (indicated as AB^c) were computed by dividing AB by the DOM concentration in the fresh feed. From a study of Thompson and Parks (1983) AB^c values of 0.42 and 0.40 were derived for two strains of Merino rams, and 0.43 and 0.39 for Dorset Horn rams and wethers, all fed *ad libitum* a diet with 10.83 MJ ME/kg DM. In a study with Merino strains (Thompson *et al.*, 1985), AB^c values for rams varied from 0.44 to 0.47 and for ewes from 0.47 to 0.52 on a diet with 10.23 MJ ME/kg DM. From the results of the long term study with crossbred sheep of Blaxter *et al.* (1982) also AB^c values can be computed. The reported parameter k in the equation $W = A\text{-}B \cdot e^{-k \cdot t}$ combined with the mean intake, which appeared to be constant throughout the whole experiment, allow calculation of AB^c as $A \cdot k$/(mean IDOM). The mean AB^c of four sheep, fed a diet containing 9.12 MJ ME/kg DM during four years, amounted 0.23 and for four animals, fed a diet containing 9.79 MJ ME/kg DM, this value was 0.26.

The estimates from the studies of Thompson and Parks (1983) and Thompson *et al.* (1985) were considerably higher than those of S and DH, which were fed a diet of approximately the same quality (10.66 MJ ME/kg DM). The estimates from the crossbred sheep (Blaxter *et al.*, 1982) corresponded well to the range in this study. The values from these different literature sources suggest a large variation in AB in ruminants, based on probably both environmental and genetic sources, which has to contribute to variation in maturation rates.

Parameter n

No breed effect was detected for parameter n, which indicated that the shape of growth and intake curves, on basis of u, were similar in both breeds for feed H. The effect of diet quality on parameter n is illustrated for the feed intake in Figure 3. At low levels of u, feed intake of DL is much lower than intake of DH, but with increasing u the curve of DL approaches DH. This implies that degree of maturity is of significance when assessing feed intake of different feeds. So far, additional information from literature, concerning the interactive effects of u and diet quality on the feed intake curve, is lacking.

Parameter k and $k/A^{-0.27}$

Equation (4) shows that, at given u, parameters k, n and u0 determine the maturation rate du/dt. There were no breed effects on n and u0, implying that breed variations in du/dt at equal u are reflected by variation of parameter k. The maturation rate (du/dt) can be regarded as a measure of growth rate in which only the numerator part is scaled by A ($du = dW/A$). According to the inter-species scaling rules k should be divided by $A^{-0.27}$ to scale also for the time element (dt). The time-scaled variable $k/A^{-0.27}$ however was higher for the Saanen breed, whereas k showed no breed effect (Table 5). This result implicates that, for these breeds, intervals of u are more closely related to unscaled age intervals than scaled intervals. The closely similar values of u for both breeds at (unscaled) birth age and weaning age (Figure 2) showed the same phenomenon for $u < u0$.

The higher feed efficiency AB of S contributed to the breed effect on $k/A^{-0.27}$ and the absence of a breed effect on k. Variation in AB due to feed quality coincided with a strong feed effect on both k and $k/A^{-0.27}$ (Table 5). Within all

groups animal variation of AB was positively correlated with k (Table 6). It should be noted however, that the use of A and u0 as fixed parameters in (3) may have led to correlations between estimate errors of parameters of (1) and (3). Such correlations might have contributed to the mentioned within-group correlations. Partial correlation coefficients of AB and k, correcting for A and n, are less affected by covariance of errors; they also showed high correlations in all three groups. It can be concluded that variation in feed efficiency AB, due to differences in breed, feed or individual animal factors, was in all cases positively correlated to variation of k and maturation rate.

Maximum feed intake (f_{max})

The feed intake/$A^{0.73}$ at $u=1$ (f_{max}) can be interpreted as the maintenance requirement for adult animals. Analogue estimates can be derived from a study with sheep of Blaxter *et al.* (1982), here requirements of adult animals amounted 31.4 DOM (g d^{-1} $kg^{-0.75}$) and were higher than the values of 28.1 for S and the overall mean value of 23.8 for WAD goats (expressed on basis of $kg^{0.75}$ instead of $kg^{0.73}$ to enable comparison). The mean value for adult WAD goats corresponded very well with the estimate of 24.3 (g d^{-1} $kg^{-0.75}$) obtained in a study with young WAD goats ranging in weight from 10 to 20 kg (Zemmelink *et al.*, 1991).

F_{max} values were similar for DL and DH, but were higher for the Saanen goats compared to DH (Table 5). Equation (5) shows that, at given u and no variation in n and u0, the variation in size-scaled feed intake, $(dF/dt)/A^{0.73}$, is determined by $A^{0.27} \cdot k \cdot AB^{-1}$ which equals f_{max}. As shown there were no breed effects on n and u0 (Table 5), and the breed contrast for f_{max} therefore reflected the difference in the scaled feed intake level in the recorded interval of u. An implication of the models (1) and (3) is that $k/A^{-0.27} = f_{max} \cdot AB$. It means that in this set of models remaining variation in $k/A^{-0.27}$, not explained by AB, is completely attributed to f_{max}. The reported breed effect on $k/A^{-0.27}$, showing a 1.32 times higher mean value for S compared to DH, therefore can be explained both by a higher feed efficiency AB of S (1.11 times higher) and a higher scaled feed intake f_{max} of S (1.18 times higher).

The breed effect on maintenance requirement at u = 1 and the scaled feed intake curve suggest a higher maintenance requirements of Saanen goats during all stages of growth. This could be related to different selection backgrounds of these breeds. Saanen goats have been kept mainly for milk production since the last century and are known as a typical dairy goats, whereas WAD goats descend from a population which have been traditionally kept for meat purposes. There is experimental evidence that among cattle breeds, maintenance requirements are higher for dairy breeds than for beef breeds (Ferrel and Jenkins, 1984). Taylor *et al.* (1986) estimated the maintenance requirement of dairy breeds to be 0.2 times greater than that of beef breeds. The underlying selective mechanisms for this trend in cattle could also have played a role for goat breeds.

Adaptation of the WAD breed to a tropical environment also might have contributed to the noticed breed effect, as observed in cattle breeds. Frisch and Vercoe (1984) reported lower metabolic rates and growth rates for Zebu cattle breeds compared to European beef breeds. They suggested that breed adaptations to environments with heat stress have resulted in lower metabolic rates and related rates of feed intake and growth. The noticed breed effects in these goats seem to indicate an interesting parallel with cattle breeds. It is obvious, however, that a comparative study with only two goat breeds does not allow conclusions with regard to general trends in goat breed effects.

Conclusions

The set of used models gave a good description of the relationships between the weight, feed intake and age data. Effects of feed quality and breed on asymptotic weight, feed intake, feed efficiency and growth, at equal levels of u, could be assessed by analysis of the derived parameters. Feed quality did not affect the asymptotic weight A of the WAD goats. Feed quality altered the shape of the feed intake curve. The feed intake at initial u started at a lower level in DL, but eventually the intake of DL approached the level of DH at full maturity. The feed efficiency AB was considerably lower for the L feed. As a result, the maturation rate (du/dt) of DL kept behind the maturation rate of DH, as expressed by their different values for parameter k.

There was a large difference in asymptotic weight between the Saanen breed (109.6 kg) and DH (48.1 kg). The shape of the scaled feed intake curve was similar for both breeds, but its magnitude was at comparable u higher for the Saanen breed. At $u=1$ the estimated IDOM of the Saanen breed was 1.18 times higher. The Saanen breed converted their feed more efficiently, having a 1.11 higher value for the AB parameter. Estimates of AB for sheep from literature indicated a wide range in AB at comparable feed qualities. There was no breed effect on parameter k, implying similar maturation rates du/dt for both breeds. If also the time element of du/dt was scaled by $A^{0.27}$, the Saanen breed showed a higher rate than the WAD breed. It can therefore be concluded that intervals of u are more closely related to unscaled age intervals than scaled intervals. Hence in this specific case, growth traits of both breeds can be better compared on basis of normal age than scaled age.

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CHAPTER 3

MULTIPHASIC ANALYSIS OF ALLOMETRY: BREED AND FEED QUALITY EFFECTS ON CHEMICAL BODY COMPOSITION IN TWO GOAT BREEDS

ABSTRACT

Breed and feed quality effects on body composition of two goat breeds were studied on basis of cross-sectional data that covered postnatal growth over a period of nearly 3 years. Two breeds were compared: 27 Saanen goats (S) and 31 West African Dwarf (WAD) goats (DH), both fed ad libitum a pelleted feed (10.7 MJ ME/kg DM). Feed effects were examined by comparing DH to another group of 31 WAD goats (DL), fed another feed (7.5 MJ ME/kg DM). At birth, group S contained slightly more water and less fat than the WAD goats. Water, protein and ash accretion were described against fatfree weight (FFW) by the simple allometric model. The allometric coefficients (b) showed a very consistent pattern among the groups, with minor effects of breed and feed. For all groups, FFW showed a decreasing water proportion toward maturity accompanied by higher protein and ash proportions.

Fat deposition was described against FFW by a diphasic allometric model. The extra phase improved the fit for S and the combined DH and DL group. Feed quality did not affect b in both phases, nor the FFW level at which the second phase started. S had a higher b than DH in the first phase, and the same in the second. S entered the second phase at a higher weight than DH, but this could be mainly attributed to their larger genetic size. The observed consistency in parameters of the diphasic allometric model among breed and nutrition groups supports the concept of distinct phases of fat growth.

MULTIPHASIC ANALYSIS OF ALLOMETRY: BREED AND FEED QUALITY EFFECTS ON CHEMICAL BODY COMPOSITIONS IN TWO GOAT BREEDS

INTRODUCTION

Studies on relative growth of tissues and organs have made widely use of the model $y = ax^b$ (or its logarithmic form), which describes relationships known in biology as simple allometry. Since its introduction as a general model for the study of relative growth (Huxley, 1924 and 1932), the allometric model has been widely adopted. Both its descriptive ability and the interpretative value of the allometric coefficient b have contributed to this. The allometric coefficient can be interpreted as the ratio of the specific growth rates of the dependent and independent variable. The size of b indicates whether components are early or late maturing relatively to other parts. Although many authors have attempted to find a theoretical justification for simple allometry, there is in general agreement on the empirical nature of this model (Gould, 1966).

Since its early application, it is also known that in some cases the allometric model is unable to fit data in extended weight ranges. On log-log plots these data show curved patterns that deviate from rectilinearity. Reeve and Huxley (1945) defined three types of such deviations: curvilinearity, segmentation into straight line-pieces and in some cases rhythmic fluctuations. Curvilinear trends are normally described by the addition of quadratic or higher polynomial components to the logarithmic allometric model. In zootechnical studies this type of model has been applied for cattle (Robelin *et al.* 1977), rabbits (Deltoro and Lopez, 1985) and pigs (Walstra, 1980). Although producing better fits, it has been acknowledged that the interpretative value of the polynomial parameters is strongly reduced, compared to the simple allometric form (Gould, 1966; Seebeck, 1968; Taylor, 1978).

Deviation from rectilinearity in log-transformed relationships can also assume a pattern where a straight line is bending at a certain stage of development towards another linear phase. Already in early studies on relative growth of molluscs, varying numbers of straight lines were fitted to a single relationship (Nomura (1926) and Sasake (1926) both quoted by Gould (1966)). The

attractive elements of this approach are the interpretative value of the simple allometric relations in each phase, and the identification of transition zones between the phases. These transitions could point at the occurrence of important physiological changes, leading to a new growth phase.

Since its first application, the multiphasic approach has received strong criticism from many authors (Lumer, 1937; Taylor, 1978; and others). This criticism was mainly directed at the use of unsound statistical methods, like the determination of transition points on basis of visual inspection. In some reports, transition zones were identified in relationships, which in other analyses were shown to be curvilinear (Ford and Horn, 1959). Moreover the validity of representing transition zones as intersections of two line-segments, suggesting abrupt physiological breakpoints, was questioned (Gould, 1966).

The multiphasic approach has nevertheless proven to be valuable in cases where the identified transition zones coincided with observable physiological changes. Examples of these are: the discontinuity in growth at moulting in crustacea (MacKay, 1942), the changes in muscle development accompanying the change in habitat of young elephant seals from land to an aquatic environment (Bryden, 1969), and the onset of puberty in rabbits inducing a new growth cycle in gonadal development (Cantier *et al.*, 1969). Use of extra polynomials in the simple allometric model to describe the preceding cases, would have obscured the true nature of the underlying growth cycles. This would have been as inappropriate as the use of multiphasic models in obviously curvilinear relationships.

In studies on chemical body composition of ruminants, which lies within the scope of this study, deviations from simple allometry were especially noted in the relation between fat accretion and total body. For cattle (Robelin *et al.*, 1977 and 1979) and sheep (Notter *et al.*, 1983) fat accretion was described in a curvilinear way by the addition of extra components to the allometric model. Robelin *et al.* (1977) however remarked that a general tendency could be observed in the development of fatty tissue in Limousin cattle. They reported a brusque change in the allometric pattern near puberty toward a higher rate of fat deposition, but did not account for this change in their model. Berg and

Butterfield (1976) referred in their study on cattle growth to the onset of a fattening phase. At this onset, fat is deposited at an increasing rate, after an previous phase of slow fat increase. They stated that early maturing cattle, having a lower mature size, enter this fattening phase at lower weights, but did not further quantify this concept in their study.

In longitudinal studies on growth composition of sheep, Searle *et al.* (1972) identified two distinct growth phases of fat deposition. When animals reached the intermediary transition zone, the fat deposition as a proportion of total gain accelerated. These data could be adequately fitted, in their arithmic form, by a model with two linear segments. Subsequent longitudinal studies in sheep, all based on indirect measurements of body composition as in the previous studies, revealed similar patterns (Searle and Griffiths, 1976; Searle *et al.*, 1988).

The strong shift to a higher rate of fat deposition might be related with the findings in a study on adipocyte numbers of sheep by Hood and Thornton (1979). Here, the onset to a high rate of fat deposition was accompanied by a sharp increase in the number of fat cells in the carcass. This number rose, within a period of two months, from an initial low level to a three times higher level with no further increases afterwards. These observations for cattle and sheep give support to the possible operation of a weight-dependent physiological mechanism, induced by reaching a certain stage of development near puberty. This mechanism might provoke a repartition of the net energy flow towards a much higher proportion of fat energy. This would imply that data of fat deposition should be analyzed by models that allow for a multiphasic development pattern.

The objective of this study was to examine the effects of breed and feed quality on the development of fat, water, protein and ash against fatfree weight in two goat breeds. The effects were assessed by comparing the parameters of models that described the developmental characteristics of each chemical component. For fat, the description was aimed at the identification of a transition zone, connecting two distinct phases of growth. For this purpose, a diphasic allometric model was applied, that identified the centre of the transition zone

between both segments, and the allometric coefficients of both phases. The data of water, protein and ash were analyzed by the simple allometric model.

MATERIAL AND METHODS

Experimental design

Data for this study were part of the results of an experiment in which individual growth, development of body dimensions, intake and chemical body composition, were recorded in goats from birth to nearly three years old. This study focused on the chemical body composition section. Procedures with regard to housing, management, feed composition, digestibility trials, growth and intake recording were described elsewhere in Chapter 1.

A brief outline of the experimental design is given here. Goats from the Saanen breed, a large sized European dairy breed, and the West African Dwarf (WAD) breed, one of smallest goat breeds, were milk-fed until weaning at 8-9 weeks. After a transition period of about three weeks with gradually decreasing supplementary hay, Saanen and WAD goats (respectively groups S and DH) were offered *ad libitum* a highly digestible, pelleted feed (feed H). In a similar procedure, pelleted lucerne (feed L) was offered *ad libitum* after weaning to a second WAD group (DL). The estimated concentrations of metabolisable energy (ME) in the dry matter (DM) of feeds H and L amounted respectively 10.7 and 7.5 MJ kg^{-1}. In all groups, only castrated male goats were used.

Animals in each treatment group were randomly selected in successive age classes to be slaughtered for body analysis. Goats were taken out at birth and at age levels of 2, 4, 6, 12, 18, 24 and the remaining at 34 months. As each age class, except for the birth group, was slaughtered at one time, some variation in age existed within each class. Table 1 summarizes the total number of animals used in the analysis and their mean weight per age class for each treatment group.

Only data of animals which showed a good health throughout the experimental period were included in the analysis. Three goats in S and three in DH suffered of an acute urinary obstruction caused by calculi in the urine. They had to be

slaughtered on top of the planned schedule (Table 1). Because these animals showed a normal growth and health until the appearance of the obstructions, and because they were taken out at the first symptoms, it was considered justified to use them in the analysis.

TABLE 1. *Number (n), mean empty-body weight (EBW) in kg and s.d. of analyzed animals for each age class[1)] and group S (Saanen breed), DH (WAD breed fed H feed) and DL (WAD breed fed L feed)*

Age class	S			DH			DL		
	EBW	s.d.	n	EBW	s.d.	n	EBW	s.d.	n
0	3.3	0.4	6	1.4	0.3	6	1.4	0.2	5
2	16.5	0.0	2	5.9	1.2	4	5.0	1.3	4
4	22.2	3.8	3[2)]	8.2	1.7	4	7.3	1.5	3
6	33.8	3.2	2	12.5	1.3	3	10.0	3.0	4
12	53.3	4.7	2	23.8	1.6	4	15.2	4.2	4
18	68.0	7.3	4[3)]	28.5	5.6	3[2)]	19.2	1.6	2
24			0	37.2	2.8	4[2)]	29.5	4.3	4
34	87.1	7.5	8	38.2	2.5	3[2)]	29.7	4.6	5

[1)] The age class numbers refer to the age in months
[2)] Including one animal dissected because of urinary calculi
[3)] Including two animals dissected because of urinary calculi

Breed sizes and slaughter range

The relationship between full liveweight (LW) and age have been analyzed in Chapter 1, which was based on the individual weekly data of a representative part of animals in this study. Strong breed effects on growth rate, associated with different adult weights, were observed. The average asymptotic value (A) of LW was estimated at 109.6 kg for S and 48.1 kg for DH. The average growth rate of DL appeared to be lower than in DH, but the estimated average A (52.1 kg) was comparable to that of DH.

In order to relate A to the slaughter range of empty-body weight (EBW) in this study, in each group the relationship between EBW and LW was described.

Fitting an allometric model to data of weaned animals, resulted in the following equations (using natural logarithms throughout this thesis):

S: $\log(EBW) = -0.316 + 1.045 \log(LW)$ $(n=21)$
DH: $\log(EBW) = -0.266 + 1.052 \log(LW)$ $(n=23)$
DL: $\log(EBW) = -0.328 + 1.045 \log(LW)$ $(n=24)$

From these equations the EBW at A (EBWA) could be estimated at 98.7 kg for S, 45.1 kg for DH and 44.8 kg for DL. The EBW range in this study covered the main part of the growth curve, as it ranged from birth to a maximum recorded EBW of 98.5 kg for S, 41.9 kg for DH and 36.3 kg for DL.

Slaughtering procedure and chemical analysis

Animals which were selected for analysis at birth, were killed within one day after birth. After being weighed, they were euthanised by injecting pentobarbiturate, and bled by severing the jugular vessels. The older animals were weighed in the morning of slaughter (final liveweight, LW), transported to the slaughter unit and weighed again just before slaughtering (slaughter weight, SW). The WAD goats of two months old were euthanised by injection of pentobarbiturate, the other goats were shot by a captive-bolt pistol and bled. After skinning and evisceration the guts were weighed before and after removing their contents. The empty body weight (EBW) was calculated as SW minus gut fill. Organs were dissected and weighed, and the carcass split. Care was taken that no body mass was lost during dissection. Finally, the total animal minus the gut contents was weighed again (EBW^*) to determine evaporation losses. Immediately thereafter the carcass was packed in tight plastic bags and frozen at -30^0 C for conservation.

The complete frozen mass of each animal was sawed into small cubicles, minced, thoroughly homogenized and sampled in a meat cutter (Berkel BV, Rotterdam) which could process 25 kg at a time. Three samples of 200 g were freeze-dried and analyzed for water, ash, nitrogen and fat. The water concentration was determined by drying freeze-dried samples at 70^0 C for 18 hours followed by 4 hours at 100^0 C.

As high fat percentages in older animals impeded accurate chemical analyses of the DM, first two freeze-dried subsamples of 50 g were extracted during 3 hours, using Soxhlet tubes and hexane as fat dissolver. The extracted samples were ground and its DM analyzed. For ash determination, samples were heated at 600^0 C in a muffle furnace during 4 hours. Nitrogen (N) was determined by the Kjeldahl method and protein was calculated as 6.25 x N. The remaining fat concentration was determined by extraction in Sohxlet tubes during one hour. The chemical composition was first calculated on basis of EBW*. The composition was recalculated on basis of EBW, on the assumption that EBW minus EBW* represented only losses of evaporated water during dissection.

Statistical analysis

The animals that were analyzed within one day after birth, offered an opportunity for a direct comparison of the two breeds at a physiologically equal stage of growth. The mean body compositions at birth of S and of the combined groups DH and DL were calculated and the differences between breed means tested (Student t-test).

Two models were defined to study the development of the chemical components over the entire weight range covered in this experiment. Data of the components water, protein and ash were for each group analyzed (PROC GLM; SAS, 1985) by the linear regression model:

$$\log(y_i) = a + b\log(x_i) + \underline{e}_i \qquad (1)$$

where for animal i, the variable y represents the chemical component (kg), parameter a is the intercept, the regression coefficient b represents the allometric growth coefficient, the variable x is the fatfree weight FFW (= water + protein + ash), and $\underline{e}$ the random error. Effects of breed and feed quality for each component were assessed by evaluating group effects within the combined data of DH + S and DH + DL respectively, using model (1). Effects on parameter a were evaluated by testing (F-test) the inclusion of group effect on parameter a in models with common parameter b. Similarly, group interactions on parameter b were evaluated in models with separate group intercepts.

The model used for analysis of fat data, was based on a general model for intersecting straight lines, proposed by Bacon and Watts (1971). This model enables a smooth continuous transition from one segment to another: in the analysis the following form was used:

$$\log(y_i) = y_0 + [b_1-(b_1-b_2)/(1+\exp(-\{\log(x_i)-x_0\}/\gamma))]\,[\log(x_i)-x_0] + \underline{e}_i \qquad (2)$$

where y is fat (kg), x is FFW (kg), b_1 and b_2 are the slopes of two linear asymptotes approached by the curve on both sides of the transition zone, γ is the curvature parameter determining this approach, y_0 and x_0 define the x and y value of the centre of the transition zone, and $\underline{e}$ the random error. The centre (y_0, x_0) coincides with the intersection point of the two linear asymptotes. Here, the slope of the curve is the mean of b_1 and b_2, and the rate of change in the curve slope is maximal. The available data were not abundant enough to study accurately the exact shape of bending in the transition zone. It was therefore decided to fix parameter γ at 0.1.

Parameters were derived by fitting model (2) in an iterative procedure for each group (PROC NLIN; SAS, 1985). Effects of breed on the allometric coefficients b_1 and b_2 were assessed by first fitting (2) to the variables of the combined data of DH and S, using a modified form of (2) with common b's and different breed estimates for y_0 and x_0. Next, the extra explained sum of squares (SS), achieved by including separate group estimates of b_1 and/or b_2 in the model, was tested (F-test) against the error term of the former model.

In a similar procedure, effects of feed quality were evaluated by first fitting (2) to the combined set of DH and DL, using a model with common parameters for both groups. In the next step, the extra explained SS, explained by models with varying combinations of group interactions on the parameters, were tested by F-tests.

RESULTS

Composition at birth

The mean birth weight and the mean composition of both breeds are listed in Table 2. The breed means reflect the mean accretion rates of the components during prenatal growth. The birth weight of the Saanen sample was more than twice the weight of the WAD breed, which illustrates the different genetic sizes of these breeds. Their chemical composition showed a very similar picture with slightly more water ($P<0.05$) and less fat ($P<0.05$) in the Saanen breed. Assuming energy contents of 39.3 MJ kg^{-1} for fat and 23.6 MJ kg^{-1} for protein (ARC, 1980), it can be calculated that the EBW of Saanen goats contained less energy (4.61 MJ kg^{-1}) at birth than the WAD goats (4.97 MJ kg^{-1}).

TABLE 2. *The mean empty-body weight (EBW) and mean chemical composition at birth of group S (Saanen breed) and group D (WAD breed, combined groups DH and DL) with their standard error*

	S (n = 6)	D (n = 11)
EBW (kg)	3.301[1)] ± 0.180	1.394[2)] ± 0.085
Water (g/kg)	765[1)] ± 3.2	757[2)] ± 1.5
Fat (g/kg)	18[1)] ± 0.8	23[2)] ± 1.3
Protein (g/kg)	165 ± 2.6	173 ± 2.6
Ash (g/kg)	39 ± 1.4	42 ± 1.8

[1),2)] Breed means with different superscript differ ($P<0.05$).

Simple allometric relationships

In Table 3 the estimated parameters of model (1) are listed for each group. All fatfree components were well fitted by (1), showing randomly distributed residuals. The composition of FFW is only slightly changing with increasing weight, as all b's were close to one, a value representing isometric growth. The three allometric coefficients of the fatfree fraction, showed a very consistent pattern in all groups. In all groups the b value of water was just below one, resulting in lower water concentrations at increasing FFW. Protein showed a reversed trend with b values from 1.055 to 1.090. The b values of ash for both WAD groups are very close to one, indicating a nearly constant proportion of ash throughout growth.

TABLE 3. *Parameter estimates, their standard errors and the residual s.d. of the allometric model[1] log(y) = a + b log(x), for each chemical component (kg) as a function of fatfree weight (kg), determined for group S (Saanen breed), DH (WAD breed fed the H feed) and DL (WAD breed fed the L feed)*

Components	S (n = 27)		DH (n = 31)		DL (n = 31)	
	est.	s.e.	est.	s.e.	est.	s.e.
Parameter a:						
Water	-0.204[2]	0.011	-0.241[3][4]	0.005	-0.251[5]	0.003
Protein	-1.873[2]	0.030	-1.749[3]	0.017	-1.713	0.013
Ash	-3.314	0.060	-3.195	0.044	-3.169	0.047
Fat	-5.665[2]	0.088	-4.094[3]	0.108	-4.185	0.124
Parameter b:						
Water	0.973	0.004	0.978[4]	0.002	0.986[5]	0.002
Protein	1.090	0.010	1.081[4]	0.007	1.055[5]	0.006
Ash	1.074[2]	0.019	1.014[3]	0.019	1.002	0.021
Fat	2.416[2]	0.028	2.210[3]	0.047	2.207	0.056
Residual s.d.:						
Water	0.019		0.012		0.008	
Protein	0.052		0.041		0.030	
Ash	0.102		0.110		0.107	
Fat	0.150		0.266		0.284	

[1] natural logarithm

[2),3)] Different superscripts 2),3) within the columns of S and DH indicate breed effects ($P < 0.05$)

[4),5)] Different superscripts 4),5) within the columns of DH and DL indicate feed quality effects ($P < 0.05$)

There was a breed effect on the b value of ash, being higher for S. The breeds had similar b's for water and protein, but differed in parameter a, indicating a breed difference in composition of FFW at equal levels of FFW. Feed quality effects on FFW were observed for the b values of water and protein, showing for the L ration a slightly higher value for water and a lower b for protein. The effects of different b's on the composition of FFW was partially reversed by parameter a for water, showing a lower value in DL. For reasons of comparison,

the results of a single-phased description of the fat component are also shown in Table 3. The high b values, all higher than 2.2, depict the different growth pattern of fat compared to the components of FFW. Both parameters a and b differed between the breeds, but not between DH and DL. For the combined groups DH and DL, parameters a and b (± s.e.) were estimated at -4.142 ± 0.082 and 2.210 ± 0.036 respectively (residual s.d. = 0.275).

The diphasic allometric model

The estimated parameters of model (2) and the residual s.d. (r.s.d.) are listed in Table 4. For all groups parameter b_2 was higher than b_1. As both b_1 and b_2 are well above 1, the ratio of accumulated fat to FFW is rapidly rising from birth on. Assessment of the effects of breed j on b_1 and b_2, using the combined data of S and DH, showed that inclusion of breed effect b_{1j} improved model (2) ($F = 12.1$; $P<0.005$). This model appeared to have the lowest r.s.d. of the models with varying combinations of b_{1j} and b_{2j} interactions. Adding also a breed effect b_{2j} to the former model did not further improve (1). The estimated b values of the best explaining model were: $b_{1\text{-}S} = 2.315 \pm 0.087$, $b_{1\text{-}DH} = 2.075 \pm 0.064$, $b_2 = 2.632 \pm 0.146$.

TABLE 4. *Parameter estimates, their standard errors and the residual s.d. of the diphasic allometric model (see text), for fat (kg) as a function of fatfree weight (kg), determined for group S (Saanen breed), DH (WAD breed fed the H feed) and DL (WAD breed fed the L feed)*

Par.	S (n=27)		DH (n=31)		DL (n=31)	
	est.	s.e.	est.	s.e.	est.	s.e.
y_0	1.518	0.702	0.650	1.040	0.761	0.732
x_0	3.042	0.281	2.221	0.462	2.319	0.318
b_1	2.299	0.051	2.085	0.080	2.070	0.091
b_2	2.719	0.128	2.532	0.243	2.699	0.329
res.s.d.	0.126		0.254		0.269	

Feed quality effects were examined by using the combined data of DH and DL. The model without any effect of feed quality on the parameters, appeared to be the one with the lowest r.s.d. among all possible forms of (1), that could be

defined with varying feed interactions. The estimated parameters for this model were: $y_0 = 0.734 \pm 0.575$, $x_0 = 2.286 \pm 0.2563$, $b_1 = 2.075 \pm 0.059$, $b_2 = 2.625 \pm 0.198$.

The r.s.d. of (2) was in all groups smaller than residuals of model (1), indicating a better fit of (2). Testing the additional explained SS of (2) against the residual variance of (1) showed a significant improvement for S ($F(2,27) = 4.47$, $P<0.05$). Since there were no feed effects in (1) and (2), results based on the combined groups of DH and DL were compared between both models. Here, model (2) was also better than (1) ($F(2,60) = 5.03$, $P<0.01$). The regression curves of model (2) for S and for the combined WAD groups are shown in Figure 1.

DISCUSSION

Composition at birth

In analyses of breed effects on growth it is essential to distinguish between non-typical variation, due to differences in genetic size and physiological stage of development, and typical variation due to true breed effects. Birth represents a physiologically comparable stage of growth, at which breeds have to be similarly developed to meet new functional demands after birth. The composition at birth therefore is a trait of interest in comparative studies of genotypes.

In this trial the composition at birth hardly differed between the breeds. Both had low fat concentrations, which in newborn ruminants is mainly consisting of brown fat (Leat and Cox, 1980) and plays an important role in non-shivering heat production just after birth. Data on birth composition of goats are scarce in literature. In a growth study of German White goats (Pfeffer and Keunicke, 1985) the water concentrations at birth were somewhat higher than in this study. They reported a composition per kg EBW of 782 g water, 146 g protein, 20 g fat and 39 g ash.

Compared to other ruminant species, the compositions in these goat breeds were similar to values given for sheep. Based on several literature sources, the

ARC (1980) reported representative values for a lamb of 3 kg EBW to be (per kg): 775 g water, 160 g protein, 40 g fat and 43 g ash. Data for cattle indicated lower water concentrations and higher protein contents. The average concentrations of three beef breeds of varying genetic size recorded by Buckley *et al.* (1990) illustrated this trend; each kg (± s.e.) consisted of 727 g ± 4 water, 204 g ± 1 protein, 26 g ± 4 fat and 43 g ± 1 ash.

Choice of FFW as the independent variable

The development after birth was analyzed by allometric relationships in which the FFW acted as the independent variable. In descriptive studies the EBW, instead of FFW, is more commonly used as the explaining variable. An important disadvantage of EBW as the independent variable is that any treatment effect, acting on the relationship between one group of components and another, may be reflected in all relationships between components and the total EBW. Such a treatment effect would suggest a direct effect on all components. In previous work with sheep and pigs, however, it has been found that treatment effects predominantly act on the relationship between two functional different entities in EBW, i.e. FFW and fat. Composition within these entities are affected to a much lesser extent, as demonstrated for instance by Elsley *et al.* (1964) in their reanalysis of earlier work of the Cambridge School. FFW can be regarded as the functional entity closely related to the metabolic active part of the body. Fat serves as a tissue for the storage of energy generated by the metabolic active part. From this point of view, it was considered justified to take FFW as the explanatory variable in this analysis.

Growth patterns of the FFW components

The allometric growth patterns of the separate components of FFW relative to total FFW, as expressed by the b coefficients, appeared to be very consistent among the groups. This consistency supports the concept of FFW as an functional entity with relatively stable relationships between its components. The feed effects in this extended weight range were small, and among the breeds there was a remarkable similarity in b values for the main components water and protein. The growth patterns of FFW in this trial were in agreement with those observed by Robelin and Geay (1978) in an analysis of composition of FFW in cattle. They reported b values for protein and water of respectively

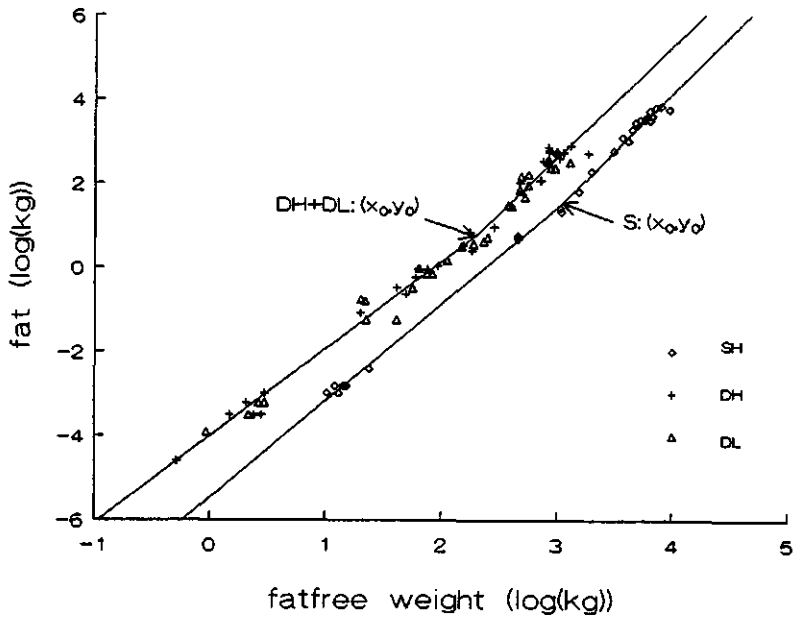

FIGURE 1. *The recorded fat (log (kg)[1)]) and fatfree weight (log(kg)[1)]) of each animal, for group S (Saanen breed), DH (WAD breed fed the H feed) and DL (WAD breed fed the L feed), together with the regression curves fitted to these data by the diphasic allometric model (see text) for group S and the combined groups DH and DL.*
[1)] natural logarithm

1.061 and 0.982; these estimates were based on a number of literature sources with varying breeds and own data. These b values for goats and cattle show a similar trend in change of composition of FFW, as observed in prenatal growth. The steadily decreasing water concentration in FFW during development is balanced by an increasing protein and ash concentration.

Parameter a of model (1) can be referred to as the (logarithmic) value of the component at FFW = 1 kg. A direct breed comparison of parameter a therefore is not very meaningful, since equal weight is not a biologically appropriate basis to compare genotypes of different genetic size. Unlike b, parameter a is both genetic-size dependent and unit dependent. The breed effects on parameter a

for protein and water, therefore, may be explained by the different breed sizes. There were no breed effects on parameter a for ash. Here size effects may be minimized by the different breed values for b.

Multiphasic allometric growth of fat

The diphasic allometric model for fat adequately fitted allometric relationships in both segments. Searle *et al.* (1972) fitted a diphasic linear model to non-transformed fat data. Their model assumed a constant composition of gain within segments. Blaxter *et al.* (1982) fitted both an allometric and a linear model to non-transformed fat data of sheep that had reached the final phase of fat growth. As both models performed equally well, showing residuals of similar size, no preference could be made. These difficulties in assessing the shape of fat deposition curves were mainly caused by the large individual variation in fat deposition of sheep. Large individual variation also complicated the choice of model in this analysis. The deposition of fat showed a segmented pattern, but the patterns within these segments did not allow a clear distinction between allometric or linear trends. In this analysis the use of a model based on allometric relationships was preferred. The allometric coefficients can be meaningfully interpreted and offer a basis for comparison with other components in this study.

The large b values for fat in relation to the fatfree components illustrate the relatively late maturing of this tissue. The increase in b in the second phase is in agreement with observed patterns in sheep (Searle *et al.*, 1972) and cattle (Robelin *et al.*, 1977; Berg and Butterfield, 1976). Genotypical variation between the goat breeds was only significant for the first growth phase of fat. The b values in the second segment were higher than in the study of Blaxter *et al.* (1982). In Blaxter's study, a value of 2.11 ± 0.30 ($n = 13$) can be calculated for wethers, slaughtered in the final fattening phase (EBW > 45 kg).

Feed quality did not affect parameter b in both segments, nor did it significantly affect y_0 or x_0 in the WAD goats. The absence of any effect on body composition is in agreement with results from comparable sheep studies. Variation in energy concentrations of diets, fed *ad libitum* to weaned lambs, did vary growth rates but did not significantly alter body composition (Andrews *et*

al., 1969; Searle and McC.Graham, 1972; Theriez *et al.*, 1982). Possibly, feed effects are too small in relation to individual variation to be detected in cross-sectional designs.

The transition zone of the diphasic allometric curve is characterized by parameters γ, x_0 and y_0. There were insufficient observations to describe accurately the exact shape of the curve in this transition zone. This necessitated the use of a fixed value for the curvature parameter γ. It is not likely that more detailed information would have revealed a sharp, abrupt break between both segments. As for most biological processes, it seems more reasonable to assume that there is a gradual, smooth change from one growth phase to another. The cross sectional design probably also contributed to a smoother and more extended bending of the curve, due to individual weight variation in x_0 and y_0.

Parameters x_0 and y_0 can be regarded as the core elements of the diphasic model. Although the smoothness of the curve was not fully known, the used model was considered appropriate to estimate the centre (x_0,y_0) of the transition zone. Here the rate of change in the curve slope is maximal, representing a stage of strong changes in fat deposition. The EBW level in this centre of transition (denoted as EBWT) can be calculated by adding the estimated FFW ($\exp(x_0)$) and fat ($\exp(y_0)$) at (x_0,y_0). Feed quality did not affect x_0 or y_0 of the WAD goats, resulting in close estimates of EBWT for DH (11.13 kg) and DL (12.30 kg). These close estimates of EBWT in entirely different groups of WAD goats demonstrate, that the identified transition zones were not merely the result of random individual variation at a certain weight level. The shown repeatability of EBWT lends support for the existence of a transitional zone connecting different phases of fat deposition.

The higher estimate of EBWT for the Saanen goats, being 25.51 kg, reflected the much larger genetic size of this breed. Searle and Griffiths (1976) also demonstrated genetic-size related differences in this trait for wether sheep of three Merino crosses. According to the genetic size scaling theory (Taylor, 1980), variation due to genetic size in cumulative variables can be eliminated by scaling by the estimated adult breed sizes (EBWA). Almost all the group

differences disappeared by applying this rule to EBWT, arriving at values of 0.26 in S, 0.25 in DH and 0.27 in DL. This indicates that almost all the breed variation in EBWT can be attributed to differences in genetic size. The similarity of the scaled values of EBWT between breeds furthermore supports the concept of distinct phases in fat deposition.

Conclusions

In conclusion, the results showed that the breeds differed slightly in body composition at birth. The components protein, water and ash could be well described by simple allometric relationships relative to FFW. Their development patterns, expressed by the allometric coefficients, showed a consistent picture among the groups. Independent of breed or feed quality, the composition of FFW showed a decreasing water concentration toward maturity, compensated by higher protein and ash contents.

The development of fat showed a segmented pattern which could be described by a diphasic allometric model. The addition of phases to the allometric model improved significantly the description of the fat data for S, and the combined groups of DH and DL. Feed quality did not affect significantly fat deposition within the two discerned phases, nor did it affect the weight level at which the final phase of fat growth was entered. The Saanen goats showed a different pattern of fat growth in the first phase, having a higher allometric coefficient than the WAD goats. The Saanen goats entered the second phase at a higher weight, but this difference could be mainly attributed to their larger genetic size. The observed consistency in the developmental characteristics of fat among the nutrition groups and the breeds supports the underlying concept of distinct phases of fat growth.

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CHAPTER 4

MULTIPHASIC ANALYSIS OF ALLOMETRY: BREED AND FEED QUALITY EFFECTS ON GROWTH OF ORGANS

ABSTRACT

Breed and feed quality effects on growth of lungs, heart, liver, kidneys, spleen, forestomachs, abomasum, duodenum, jejunum/ileum and the humerus bone were examined by both monophasic and multiphasic analysis of their growth relative to fatfree weight (FFW). Two breeds were compared, 27 Saanen (group S) and 31 West African Dwarf (WAD) goats (group DH), both fed ad libitum pellets (10.7 MJ ME/kg DM). Feed effects were examined by comparing DH to 31 WAD goats (group DL), fed another pellet ad libitum (7.5 MJ ME/kg DM). Monophasic and multiphasic allometric models were fitted to cross-sectional data of animals ranging in age from birth to an age of nearly 3 years.

Analyzed organs were consistently single-phased or diphasic in both breeds. The same consistency, except for heart, was observed among both feed quality groups. Only heart growth (for S and DH only), and abomasum and humerus were single-phased. The allometric coefficients of the diphasic organs indicated in their first phase a proportional increase of organ and thereafter a proportional decrease. The goats in DL developed a larger digestive tract, heart, kidneys and liver than goats of equal weight in DH. The breeds had very similar allometric coefficients, which differed only for the second phase of the lungs and jej./ileum, and for both phases of the liver. The main part of the breed variation was expressed by genetic size-dependent parameters. The consistently higher weight levels at transition for group S reflect the larger genetic size of the Saanen breed.

MULTIPHASIC ANALYSIS OF ALLOMETRY IN GOATS: EFFECTS OF BREED AND FEED QUALITY ON THE GROWTH OF ORGANS

INTRODUCTION

The relative size and maturing patterns of organs are closely interlinked with the different functional demands that arise during the successive developmental stages. A well known example in ruminants is the relatively strong developed abomasum at birth, and the rapid development of the forestomach complex at the introduction of solid feed to suckling animals. Beside developmental stage also nutritional factors are known to affect organ growth. Elevated metabolic rates, induced by raising alimentation levels (in terms of offered quantities), were shown to increase the relative weight of visceral organs in pigs and sheep (Koong *et al.*, 1983). Very little is known, however, of feed quality effects of *ad libitum* offered feeds. Feed quality effects on organ growth might be of interest in relation to maintenance and growth efficiency, as a large part of the energy expenditure can be attributed to visceral organs (Ferrel and Jenkins, 1985; Pekas and Wray, 1991).

The relative size and maturing patterns of organs were shown to be subject to genotypical variation. In cattle, selection of dairy and beef genotypes has resulted in higher proportions of visceral organs, heart and lungs in dairy breeds (Jones *et al.*, 1985). Lilja (1983) showed that bird species can be characterized by different development patterns of digestive organs and liver, and associated the relatively early development in some species of these organs with a high growth rate capacity. Similarly, genotypical differences in organ development between ruminant breeds could provide a basis for varying growth patterns, and therefore deserve attention.

Studies on growth patterns of organs generally make use of the allometric model $y = ax^b$ or its logarithmic linear form $\log(y) = \log(a) + b \log(x)$, describing relationships known as simple allometry. Parameter b is normally called the allometric coefficient and can be interpreted as the ratio of the specific growth rates of y and x. The size of b indicates whether y is early

($b<1$) or late ($b>1$) maturing relative to x. However, in studies on postnatal growth of organs in rabbits (Cantier *et al.*, 1985), birds (Lilja, 1981 and 1983), and sheep (Bénévent, 1971) the simple allometric model did not hold for the whole weight range. The observed patterns led these authors to fit different line pieces to successive weight ranges, where each segment has its own allometric coefficient. This multiphasic approach allows for an interpretation on basis of the allometric coefficients and enables the identification of possible growth phases.

In a cross-sectional study of the chemical body composition of two goat breeds (Chapter 3) the fat component showed two growth phases when described against the fatfree weight. This finding implicates that care has to be taken in the interpretation of growth phases in organs when expressed against the total body. The phases in organ growth in the above mentioned studies were all based on a description against *total* body weight. Here the identified phases could have been merely a reflection of the diphasic pattern of fat deposition against the fatfree weight. To avoid such effects it seems therefore more appropriate to use fatfree weight as the explanatory variable in the allometric models that describe the growth patterns of organs.

The objective of this study was to quantify the effects of breed and feed quality on the growth pattern of main organs relative to the fatfree weight in two goat breeds. For each organ the effects were assessed by comparing parameters from monophasic allometric models or where appropriate from multiphasic allometric models. As a reference to skeletal development also the growth pattern of the humerus was included in the analysis.

MATERIAL AND METHODS

Animals and experimental design

Data were from an experiment in which individual growth, development of body dimensions, intake and chemical body composition were recorded in goats from birth to nearly 3 years old. Details of this experiment with regard to

management, feed composition, growth and intake recording were described before in Chapter 2.

Briefly, castrated male goats from the Saanen breed, a large sized European dairy breed, and the West African Dwarf (WAD) breed, one of the smallest goat breeds, were milk-fed until weaning at 9 weeks. The levels of weaning weight in terms of fatfree weight (FFW) were 10 kg for the Saanen breed and 5 kg for the WAD breed. After a transition period of 3 weeks with gradually decreasing supplementary hay, Saanen and WAD goats (respectively groups S and DH) were offered *ad libitum* a highly digestible, pelleted feed (feed H; 10.7 MJ ME/kg DM). In a similar procedure, pelleted lucerne (feed L; 7.5 MJ ME/kg DM) was offered *ad libitum* to a second WAD group (DL).

Animals in each treatment group were randomly selected in successive age classes to be slaughtered for body analysis. Goats were taken out at birth and at age levels of 2, 4, 6, 12, 18, 24 and the remaining at 34 months. In total 27 animals were dissected in group S, 31 in DH and 31 in DL. The empty body weight (EBW) range in this study covered the main part of the growth curve. The mean adult EBW was estimated in an earlier analysis (Chapter 3) at 98.7 kg for S, 45.1 kg for DH and 44.8 kg for DL. In this study EBW ranged from birth weight to a maximum recorded EBW of 98.5 kg in S, 41.9 kg in DH and 36.3 kg in DL.

Determination of organ and bone weights

The procedures of slaughtering and determination of the chemical composition of the total body were described in Chapter 3. After slaughter the animals were exsanguinated, the oesophagus ligated and the full gastrointestinal tract taken out. Double ligatures were placed between abomasum and duodenum, between duodenum and jejunum, and between ileum and caecum. The segments of the tract were separated by cutting between the ligatures, and the surrounding fat depositions were removed. The segments were weighed and drained of their contents. The following parts were weighed empty: forestomach (the combined weight of rumen, reticulum and omasum), abomasum, duodenum and the combined jejunum and ileum (jej./ileum).

The lungs, heart, liver, spleen and kidneys were removed and weighed. The heart was emptied of blood, and its vessels trimmed at the basis of the heart. The gall bladder was removed from the liver before weighing. The right humerus bone was dissected, made free of adhering tissues, and weighed.

Models and statistical analysis

Both a monophasic and a diphasic model were fitted to the data of organ weight and FFW. The monophasic or simple allometric model was applied in its (natural) logarithmic form:

$$\log(y_i) = a + b \log(x_i) + \underline{e}_i$$

where y_i is the organ weight (kg) of animal i, x_i the FFW (kg), parameter a the intercept, b the regression coefficient or allometric growth coefficient and $\underline{e}_i$ the random error. The diphasic model was based on a general multiphasic linear regression model proposed by Koops and Grossman (1993). In the analysis the following form was used:

$$\log(y_i) = a_1 + b_1 \log(x) - (b_1 - b_2)\, r \log[1 + e^{\{\log(x)-c\}/r}] + \underline{e}_i$$

where y_i is the organ weight (kg) for each animal i, x_i is FFW (kg), a_1 is the intercept, b_1 and b_2 are the regression coefficients of the two linear segments approached by the curve on both sides, r is the smoothness parameter, c the value for log(x) in the centre of the transition zone, and $\underline{e}_i$ the random error.

The diphasic model allows a continuous smooth transition between linear segments. Due to the symmetrical form of the transition zone, the rate of change in the curve slope is maximal for c, and the slope at c lies just in between b_1 and b_2. There were not enough data to study accurately the exact shape of bending in the transition zone, therefore the curvature parameter r was fixed at 0.1.

The monophasic model was fitted for each group (PROC GLM; SAS, 1990). Parameters of the diphasic model were estimated in an iterative procedure for

each group (PROC NLIN, method DUD; SAS, 1990). To avoid too large exponential values in the diphasic model, $(r \log[1 + e^{\{\log(x)-c\}/r}])$ was set to 0 for $\{\log(x)-c\}/r < -10$ or to $\{\log(x)-c\}$ for $\{\log(x)-c\}/r > 10$ as described by Koops and Grossman (1992). To assess the improvement of fit by the diphasic model, the extra explained sum of squares (SS) was tested by an F-test against the mean square error of the monophasic model.

Feed quality and breed effects were assessed on basis of the best phasic model. For components showing a monophasic pattern, effects of breed and feed quality on parameters a and the allometric growth coefficient b were examined by means of F-tests. For the diphasic model effects of feed quality were examined by comparing parameters of group DH and DL. First a model with common parameters was fitted to the combined data set. Next, models with varying combinations of separate group parameters and common parameters were fitted to the combined set, to derive the best explaining model with the lowest residual standard deviation (r.s.d.). The extra explained SS of the best model was tested in an F-test against the mean square error of the model of the first step.

Breed effects on diphasic growth patterns were examined in a similar procedure. According to the genetic size-scaling theory (Taylor, 1980), genotypical variation can be split up in a genetic-size component and a component representing typical size-independent variation. In this study the analysis was restricted to testing the size-independent effects represented by the allometric coefficient b_1 and b_2. The large difference in breed size (Chapter 2) was accounted for by including separate breed estimates for parameters a_1 and c in all models. In the first step, a model with common parameters for b_1 and b_2 was fitted to the combined data set of S, DH and DL. For components where feed quality effects were demonstrated for one or more parameters, separate parameters were included for DH and DL. In case of feed effects on b_1 or b_2, b parameters of S were set equal to those of DH. In the next step, models with varying combinations of different b parameters for breeds and common b parameters were fitted. The best fitting model was compared to the initial model, using an F-test to test breed effects.

RESULTS

The monophasic versus the diphasic model

The inclusion of a second phase improved the fit for all organs ($P < 0.05$) except heart, abomasum and the humerus (Table 1). Residuals of the diphasic model showed distribution patterns which were not conflicting with the assumed linear nature of the model segments. For 9 out of 10 components the best model had the same number of phases in all three groups. Only for the heart results differed between groups. Although r.s.d.'s of the diphasic model were smaller than those of the monophasic model in all groups, only for group DL the extra phase significantly improved the fit of the heart data.

TABLE 1. *The results of F-tests applied to groups S (Saanen breed), DH (WAD breed fed the H feed) and DL (WAD breed fed the L feed), assessing the improvement of fit by adding a second phase to the allometric relationship between organ/bone mass and fatfree weight*

	S (n = 27)	DH (n = 31)	DL (n = 31)
Lungs	**	**	**
Heart	ns	ns	*
Liver	**	**	**
Kidneys	*	**	**
Spleen	**	**	**
Forestomachs	**	**	**
Abomasum	ns	ns	ns
Duodenum	*	*	**
Jej./Ileum	**	**	**
Humerus	ns	ns	ns

In general the b values of the diphasic organs were higher than one in the first phase and declined to values smaller than one in the second (Table 2). This shift depicts a general growth pattern in which initially the organ mass is proportionally increasing in the FFW, followed by a proportional decrease.

TABLE 2. *Estimates and standard errors (s.e.) of parameters a_1, c, b_1, b_2 of the diphasic allometric model (see text) describing organ growth relative to fatfree weight, for groups S (Saanen breed), DH (WAD breed fed H feed) and DL (WAD breed fed L feed); for components without a diphasic pattern, parameters a and b of the monophasic allometric model are listed*

Organ	Par.	S		DH		DL	
		est.	s.e.	est.	s.e.	est.	s.e.
Lungs	a_1	-4.16	0.10	-4.11	0.04	[1]	
	c	2.80	0.19	1.46	0.17	[1]	
	b1	[2]		1.03	0.06	[1]	
	b2	0.24	0.12	0.51	0.04	[1]	
Heart[3]	a_1	-		-		-4.92	0.05
	c	-		-		2.11	0.29
	b_1	-		-		0.86	0.04
	b_2	-		-		1.15	0.09
Liver	a_1	-3.78	0.10	-3.76	0.06	[1]	
	c	3.18	0.19	0.88	0.20	[1]	
	b_1	1.13	0.05	1.50	0.17	[1]	
	b_2	0.27	0.22	0.85	0.03	0.93	0.03
Kidneys	a_1	-5.02	0.08	-4.93	0.04	[1]	
	c	2.99	0.23	1.88	0.22	[1]	
	b_1	[2]		1.00	0.04	[1]	
	b_2	[2]		0.54	0.08	0.72	0.06
Spleen	a_1	-7.57	0.27	-6.73	0.09	[1]	
	c	2.21	0.30	1.27	0.27	[1]	
	b_1	[2]		1.83	0.22	[1]	
	b_2	[2]		0.92	0.06	[1]	
Forestomach	a_1	-6.16	0.10	-5.12	0.06	[1]	
	c	2.80	0.11	1.75	0.05	1.96	0.10
	b_1	[2]		2.02	0.05	[1]	
	b_2	[2]		0.83	0.08	[1]	

***Table 2** Continued*

Organ	Par.	S		DH		DL	
		est.	s.e.	est.	s.e.	est.	s.e.
Duodenum	a_1	-7.88	0.20	-7.59	0.12	[1]	
	c	2.87	0.23	1.89	0.21	2.12	0.19
	b_1	[2]		1.30	0.10	[1]	
	b_2	[2]		0.12	0.19	[1]	
Jej.\Ileum	a_1	-3.91	0.11	-3.56	0.06	[1]	
	c	3.10	0.11	1.80	0.12	1.98	0.11
	b_1	[2]		1.17	0.05	[1]	
	b_2	-0.94	0.29	-0.04	0.10	[1]	
Heart[3]	a	-4.72	0.03	-4.95	0.03	-	
	b	[2]		0.91	0.01	-	
Abomasum	a	-4.52	0.04	-4.85	0.04	-4.66	0.04
	b	[2]		0.89	0.02	[1]	
Humerus	a	-4.63	0.02	-4.90	0.02	[1]	
	b	[2]		0.81	0.01	[1]	

[1] If no feed quality effects are present, common estimates for DH and DL are listed in the column of DH
[2] If no breed effects are present, common estimates for S and DH are listed in the column of DH
[3] The diphasic model for the heart was fitted to group DL only

The heart growth in DL represented a notable exception from this trend, demonstrating a reversed picture.

Effects of feed quality

Feed quality differences between DH and DL were introduced after weaning. Feed quality effects may therefore be expected to occur only after weaning ($\log(FFW) > 1.6$). For liver and kidneys, however, the best fitting model for the combined groups contained different b_1 values, suggesting differences from birth on. As this effect has to be attributed to random sources, it was

considered justified to use in the analysis a model with a common b_1 which appeared to be the next best fitting model.

As indicated before, heart growth showed a statistical significant diphasic pattern only for group DL, but there was a tendency towards a similar pattern in S and DH. Fitting the diphasic model to data of S and DH resulted in b_2 values that were higher than b_1; for S, b_1 and b_2 were 0.83 and 1.00 respectively, and for DH 0.87 and 0.96. The b_2 estimate of DL was significantly higher than the value of DH but estimates of a, b_1 and c were similar.

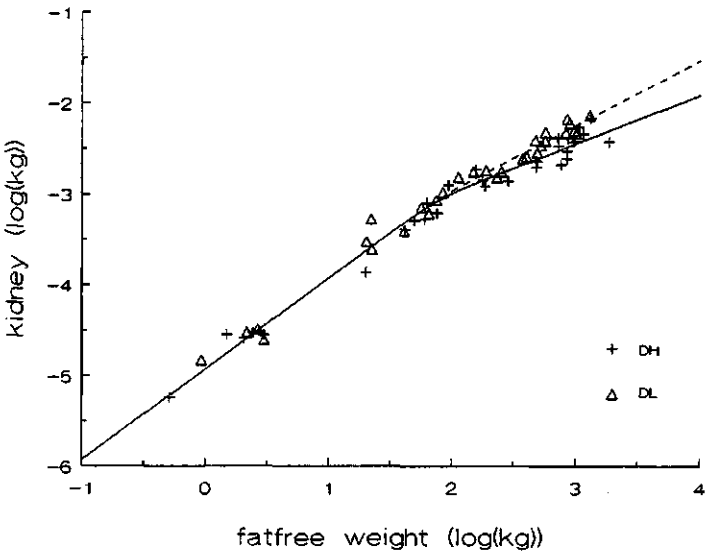
Two other types of feed effects can be distinguished in Table 2. The first type is represented by higher b_2 estimates of DL for liver and kidneys, whereas the other parameters were not affected. The second type shows a feed effect on parameter c, being higher in DL for the forestomach, duodenum and jej./ileum. Figure 1a and 1b illustrate both types of feed effects for the kidneys and the forestomach respectively. Both effects resulted in higher organ weights in the second phase for animals fed the low quality feed. Feed quality also affected the single-phased abomasum development (Table 2), again showing a relatively higher weight level for DL.

Effects of breed

The growth patterns as expressed by parameters b_1, b_2 and b appeared to be in general very much alike in both breeds. Only for the liver, b values differed for both phases, whereas in case of the lungs and jej./ileum the b_2 estimate was lower for the Saanen breed. The negative b_2 value of the jej./ileum indicated a reduction in tissue mass during the second phase, which was especially pronounced in the Saanen breed (Figure 2).

Parameter c reflected the large breed difference in genetic size, showing consistently higher values for group S. In terms of ranking of parameter c among the organs, the position of the estimate for liver differed markedly between the breeds, being the highest in S and the lowest in DH. For the other organs the ranking was similar, starting with the spleen, followed by lungs and forestomach, and ending with kidneys and intestines.

a)



b)

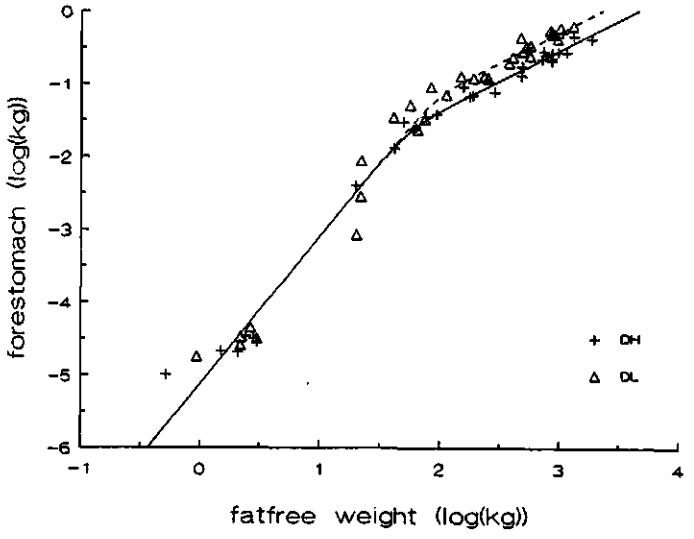


FIGURE 1. ***a)*** *The values of kidney weight (log(kg)[1)]), and* ***b)*** *of forestomach weight (log(kg)) against the fatfree weight (log(kg)) of each animal in group DH (WAD breed fed the H feed) and DL (WAD breed fed the L feed), and the regression curves fitted to these data by the diphasic allometric model (see text) for both groups.*

[1)] *natural logarithm*

DISCUSSION

Use of the multiphasic allometric model

In this study the multiphasic approach was considered to be the most appropriate one to describe the observed log-log patterns in which apparently linear segments were smoothly interlinked. It is realized that, in general, care has to be taken in the biological interpretation of the identified phases and their transitions (Gould, 1966). The use here of the term 'phase' was aimed at the identification of the linear segments which differ in slope. This slope, represented by the allometric coefficient, summarizes the priority in growth of the component relative to the total growth in the observed weight range. Hence, changes in phase basically indicate redistributions in growth priorities between components. This not necessarily implies that components undergo major morphological or functional changes at transition, although the possibility exists that phase changes are induced by such factors.

Without doubt the data of part of the organs could also have been described in a mathematically satisfactory way by other modifications of the simple allometric model. Several modifications are presented in literature that account for deviations from rectilinearity, like the addition of polynomial components. The gain in flexibility, however, is generally counterbalanced by a loss of the interpretative value of the model parameters (Gould, 1966; Taylor, 1978). In the multiphasic approach there is no such loss. The slope parameters or allometric coefficients may be interpreted similarly to the monophasic model, expressing the ratio of the specific growth rates, and the meaning of the transition and smoothness parameter are clear. This interpretability facilitates a detailed understanding of the nature of genotypical and environmental effects on the growth patterns of organs.

Diphasic growth patterns

The allometric coefficients of the circulatory and digestive organs with a diphasic growth pattern decreased to values lower than one in their second phase (except for the heart in DL). Growth studies in sheep indicated comparable patterns for most of these organs. In a cross-sectional study with Merino sheep that ranged in weight from birth weight to 25 kg EBW, Bénévent

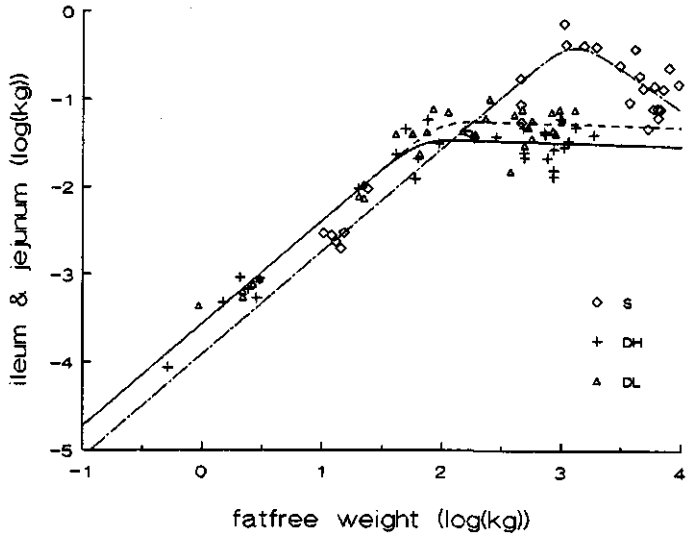


FIGURE 2. *The values of ileum and jejunum weight (log(kg)[1)]) against the fatfree weight (log(kg)[1)]) of each animal in group S (Saanen breed), DH (WAD breed fed the H feed) and DL (WAD breed fed the L feed), and the regression curves fitted to these data by the diphasic allometric model (see text) for each group.*
[1)] natural logarithm

(1971) found a similar trend in diphasic allometric growth patterns (relative to EBW) for the total digestive tract, kidneys and spleen. As for groups S and DH, the heart growth of these sheep was single-phased (b = 0.79). Contrary to the goat breeds, however, liver growth was also single-phased (b = 1.12), which might be related to the much shorter weight range in this study. In a study with two sheep breeds and their cross (5 to 55 kg LW), Kirton *et al.* (1972) observed deviations from log-rectilinearity (relative to starved LW) for the rumen, reticulum, the small intestine, liver and spleen, but not for the heart, lungs and kidneys. The slopes of the rumen and reticulum showed a decreasing trend but remained higher than one, whereas the other organs eventually turned below one. It is difficult to assess whether these deviating results for lungs and kidneys reflect true differences with the findings reported here, or are merely the result of being based on different parts of the growth curve. Diphasic patterns of organ growth were also described in rabbits (Cantier *et al.*, 1969; Deltoro and Lopez, 1985) and birds (Lilja 1981 and 1983).

The forestomach complex showed in its first phase the highest allometric coefficient ($b_1 = 2.02$) of the studied components. The b_1 values of duodenum and jej./ileum were considerably smaller but still higher than one, while the single-phased abomasum was proportionally decreasing from birth on. This strong difference in relative growth of the forestomach and the abomasum depicts the important digestive role of the abomasum during the immediate postnatal period of milk feeding, requiring a well developed organ at birth, whereas the forestomach development is accelerating for the solid food phase only after birth. During the second phase of growth of the forestomach, its evolution was much more in balance with abomasum growth, having b values of comparable magnitude. The levels for FFW at which the diphasic components of the digestive tract entered the second phase are lying close to each other, which is in line with their narrow functional relationships.

Unlike all other components the jej./ileum was not growing any more after transition, even showing a considerable mass reduction in group S. This phenomenon has been observed before in sheep by Hammond (1932), Butterfield *et al.* (1983), Butterfield *et al.* (1984) and McC.Graham *et al.* (1991). In our study the length of the combined jejunum and ileum was also recorded. This length showed a diphasic pattern with transition zones comparable to the mass equivalent. For groups S, DH and DL the b_1 values were 0.51, 0.39 and 0.54 respectively and the b_2 estimates 0.06, 0.19 and 0.08. The latter values tend to an almost stable total length and indicate no decrease. Apparently the mass reduction was accomplished by a diminished diameter or wall thickness. If there is a functional relationship between tissue mass and intake, a decreased intake might explain the reduction, yet the recorded feed intake of part of the involved animals showed no decreasing feed levels towards maturity (Chapter 2). There are no indications in literature of the occurrence of major physiological/functional changes in the digestive function of the small intestine during postnatal growth. Hence, the physiological background of this reduction of jej./ileum mass, where at the same time forestomach and abomasum continue growing, are unknown.

The second highest b_1 value (1.83) was recorded for the spleen. The length of this phase was relatively short compared to other diphasic organs, as it entered

the second phase ($b_2 = 0.92$) before weaning in both breeds. A similar decrease in b values was found by Bénévent (1971) in sheep: $b_1 = 1.72$ and $b_2 = 0.72$. The size of the b values of the study of Bénévent, however, are not directly comparable to b values in this study because they were expressed relative to EBW. The strong early increase of this lymphatic organ could be related to its role in the immune system, which needs to be set up during the first stage of postnatal growth.

Unlike most of the studied organs and fat, the skeletal growth, exemplified by the humerus, showed no multiphasic nature relative to FFW and was early maturing (Table 2). In many dissectional studies that compared growth of muscle (being the main part of FFW) and bone, these early maturing characteristics of bone have been observed (Berg and Butterfield, 1976 and others). The absence of any change in growth priority of bone relative to muscle is in line with the generally observed strict functional relationship between muscle mass and bone mass to ensure internal stability and mobility throughout postnatal life.

Effects of feed quality

Feed quality had an important effect on the growth of the digestive tract, heart, liver and kidneys. Differences were considerable between DH and DL. When compared at the weight level associated with the start of the second fat deposition phase, being 9.83 kg FFW (Chapter 3), the estimated value of the forestomach amounted 409 g for DL against 320 g for DH, and the liver weight 322 for DL against 288 g for DH. The larger tissue mass of the digestive and circulatory organs of animals in group DL could imply that the efficiency in utilization of metabolizable energy is negatively influenced, because a relatively larger proportion of energy intake has to be spent to these organs. It might therefore be possible that differences in organ mass could provide a physiological basis for part of the variance in utilization of metabolizable energy between feeds.

The feed effect on the growth of heart and kidney is could be related to a possibly larger blood volume of animals in DL. Analysis of additional data of collected blood at slaughter support this concept. They showed a simple

allometric relationship between blood and FFW for animals fully adapted to the treatment rations (FFW > 5.75 kg). The groups DH and DL had a common allometric coefficient of 0.95, but differed for parameter a, being -2.87 for DH and -2.71 for DL. This difference indicates a larger blood volume in DL when compared to animals with equal weight in group DH. The b value closely resembled those of the heart (Table 2). Its agreement was even better when the separate b values of collected blood were considered for DH (0.91) and for DL (0.98), although these values, as mentioned before, did not significantly differ ($P>0.05$). It is emphasized that for conclusive evidence a direct measurement of the total blood volume would have been needed. Even so, the observed phenomena in the circulatory organs point at an possibly interesting physiological effect of feed quality.

Effects of breed

The two breeds demonstrated very similar single-phased and diphasic development patterns except for the liver which showed markedly different b values in both phases. The observed similarity in b values implies that the breed effects were mainly expressed by parameters a and c. Variance of parameters a and c can be attributed both to effects of genetic size and size-independent breed effects. Parameter c represents weight at transition from one phase to another; this transition can be interpreted as an equivalent developmental stage among animals. Values of parameter c show systematic higher weight levels for the Saanen breed compared to the WAD breed (Table 2). The higher weight levels indicate that the Saanen breed is genetically larger. This is in agreement with the more than two times higher asymptotic weight level of this breed (Chapter 2).

A genetic-size scaling procedure would be needed to correct for genetic size effects on the organ size of both breeds. Only after size-scaling it is possible to assess whether organs are relatively stronger developed for a specific breed. For a proper inter-breed scaling procedure, information is required of the overall inter-breed relationships between organ size and measures of overall genetic size. These relationships are known to be mainly allometric (i.e. non-isometric) between species (Peters, 1983), which means that organ sizes of differently sized genotypes should not be compared in terms of proportions of a reference

weight. Sofar inter-breed relationships for scaling of organ growth are not very well established within species. Because in this study only two breed are included, they cannot be derived from this study. Once such relations are developed, the identified transition zones of diphasic organs (denoted by parameter c) could serve as a comparable stage of maturity for scaling of organ size.

The overall picture of organ growth that emerges in both breeds is that of a relatively strong development relative to FFW in the early stage of postnatal growth, followed by a phase of moderate growth. A reversed pattern was shown for the growth of fat which accelerated in its second phase (Chapter 3). Comparison of the FFW levels associated with the transition zones of both tissue types shows that the second phase of fat growth started after those of the organs in DH and DL (parameter c of fat was 2.29 for both DH and DL). For group S, the transition zone of fat was similarly located at the end of the range for organs, although fat represented not the final transition zone as liver and jej./ileum showed slightly higher values of c. The overall pattern that emerges from the size of allometric coefficients and the ranking of transition zones is consistent with a growth strategy in which first priority is given to organs that determine the intake and growth capacity, followed by storage tissues.

Conclusions

In conclusion, analyses of organ growth relative to FFW by monophasic and diphasic allometric models showed that growth patterns were consistently single-phased or diphasic in both breeds. The same consistency was observed among both feed quality groups except for heart growth. This consistency, irrespective of genotype and feed quality, indicates that the observed monophasic or diphasic pattern reflects a fundamental characteristic of their growth, and support the use of multiphasic models in analyses of organ growth. The diphasic organs showed in their first phase a proportional increase relative to FFW ($b_1 > 1$ and thereafter a decrease ($b_2 < 1$). The jej./ileum component was not only proportionally decreasing in the second phase but also absolutely, which was especially pronounced in the Saanen goats.

The goats which were fed the lower feed quality (DL) developed a larger digestive tract, heart, kidneys and liver compared to goats of equal weight in DH. It is suggested that this phenomenon might explain differences in feed efficiencies. The larger size of kidneys and heart in group DL could be related to a possibly larger blood volume. The breeds had very similar b values, which differed only for the second phase of the lungs and jej./ileum, and for both phases of the liver. The main part of the breed variation was expressed by parameters a and c. The consistently higher levels of parameter c for group S reflects the larger genetic size of the Saanen breed. Knowledge of inter-breed relationships between organ size and genetic size is required to assess whether organs are stronger developed in a specific breed.

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CHAPTER 5

MULTIPHASIC ANALYSIS OF ALLOMETRY: A LONGITUDINAL STUDY OF BREED AND FEED QUALITY EFFECTS ON BODY DIMENSIONS

ABSTRACT

Breed and feed quality effects on chest girth (CG), length of trunk (TL) and ulna (UL) of goats were examined by monophasic and multiphasic analysis of their growth relative to weight (LW). Two breeds were compared, 15 Saanen (group S) and 12 West African Dwarf goats (DH), both fed ad libitum pellets (10.7 MJ ME/kg DM). Feed effects were examined by comparing DH to 9 dwarf goats (DL), fed another pellet ad libitum (7.5 MJ ME/kg DM). Data ranged from birth to at least 55% of the asymptotic LW and were analyzed on individual longitudinal basis. Allometric coefficients from the monophasic allometric model indicated proportional enlarging of CG, and decreasing of TL and UL. The diphasic model described CG better than a monophasic model. Allometric coefficients increased from the first (0.31) to the second phase (0.45), and were not affected by breed or feed. Breed estimates of transition zones between phases in CG might serve as indicators of genetic size. TL and UL could not be fitted adequately by a diphasic model. However, separate analyses of preweaning and postweaning growth improved the overall monophasic fits in most cases. Monophasic residuals of UL showed systematic changes in postweaning growth patterns, and indicated the absence of epiphyseal closure in these castrated animals. Comparison of TL/UL ratios at different degrees of maturity indicated that both breeds had similar ratios, and did not lend any support to achondroplasia as a physiological basis for dwarfing of the WAD breed.

MULTIPHASIC ANALYSIS OF ALLOMETRY IN GOATS: A LONGITUDINAL STUDY OF BREED AND FEED QUALITY EFFECTS ON BODY DIMENSIONS

INTRODUCTION

Ruminants undergo considerable changes in body shape during prenatal and postnatal growth toward maturity. Hammond gave a clear illustration of such shape transformations in his book 'Farm animals' (Hammond, 1940). He showed charts with series of photographs of sheep and cattle at differing growth stages. The photographs were scaled to similar withers' height to eliminate variation in body size. They demonstrate that new-born animals have relatively long legs and short, shallow bodies compared to full-grown animals.

Geometrical similarity among bodies is represented by equal values for every possible ratio of equidimensional measurements; any difference in ratio between bodies implies a different shape. Among similarly shaped bodies, the (one-dimensional) linear measurements have to be proportional to the cube root of the volume, or body weight if one assumes its specific gravity to be constant. The use of the simple allometric model $y = aW^b$ (or its log-linear form) in analyses of growth of linear dimensions (y) relative to weight (W), therefore, is a very descriptive one with regard to shape. In this equation deviation of parameter b from 1/3 indicates change in body shape. For example the above mentioned tendency in height development can be well summarized by b values of 0.24 and 0.26 for Jersey and Holstein cattle respectively (Brody, 1945).

The available literature on growth studies of linear body dimensions shows an almost exclusive use of the allometric model for analysis. This can be easily understood in view of the earlier mentioned interpretation of parameter b, but also because of two other favourable properties. Parameter b is independent of animal size, allowing direct comparison of genotypes which differ in mature size, as exemplified before by comparing height development of the Holsteins and the considerably smaller Jersey breed. If relationships are simple allometric throughout, parameter b characterizes growth patterns irrespective of the developmental stages of y and W. This considerably simplifies genotype

comparison as no specific growth stage needs to be defined as a reference basis for comparison.

Yet in these attractive properties hides a risk of ignoring systematic deviations from the model. It is doubtful whether the simple allometric relation holds for all stages of growth in linear dimensions. Brody (1945) pointed at systematic residual patterns in fits of the allometric model to cross-sectional data of weight versus height/heart girth for different cattle breeds. Increase in bone length (which determines most linear measurements) is generally assumed to stop after sexual maturity (Short, 1980), whereas total weight gain still may continue. Wiener and Hayter (1974) noted in a study with different sheep breeds that the within-breed slope of the tibia against weight was considerably steeper at earlier stages of growth than at later stages. Both in cross-sectional studies of pigs (Walstra, 1980) and rabbits (Deltoro and Lopez, 1988) relationships between limb bone lengths and carcass length deviated from simple allometry. They were better described by adding a quadratic component to the log-linear model. Neglecting deviations from simple allometry may easily lead to wrong conclusions in genotype comparisons, especially when growth stages are not exactly similar.

Deviations from simple allometry may occur when body components pass distinct phases of growth, which can be described by a multiphasic allometric model. A multiphasic allometric model preserves the interpretative value of the simple allometric relations in each phase, and identifies transition zones between them. Diphasic allometric models adequately described growth of fat and several organs relative to fatfree weight in two goat breeds (Chapter 3 and 4). In these studies the diphasic model allowed a comparison of allometric coefficients of the breeds for each phase, and indicated how breed size differences affected the weight level at transition.

It is unknown to what extent multiphasic patterns are of importance in growth of linear body dimensions. Their possible existence might be of interest in relation to improving determination methods for genetic size, which is used as a scaling factor in the genetic size-scaling theory (Taylor, 1980; Chapter 1). In this theory genetic size is defined as the inherent factor that regulates the scale

of growth from conception to maturity. This genetic size factor is usually quantified by the 'adult' or maximum weight of an animal. Adult weight, however, is difficult to estimate accurately from weight-age relations at early stages of growth, particularly when environmental conditions are fluctuating (Chapter 1). There is a need for a more accurate and practical measure of genetic size, especially when genetic differences are small (Taylor, 1985). Multiphasic growth characteristics, in principle, offer a promising perspective for genetic size definition, as phasic patterns are not easily changed by environmental factors (Chapter 3). Bone length growth may be well suited for this purpose. Length can be easily measured externally. Genetic size might be determined as the weight level at which bone enters a subsequent developmental phase. Thus transition zones in multiphasic growth patterns could serve as indicators of genetic size.

The objective of this study was to examine the growth pattern of three linear body measurements - chest girth, trunk length and ulna length - in two goat breeds from birth to maturity. The growth relative to weight was described, for each individual, by both the simple allometric relation and a diphasic allometric relation. Effects of breed and feed quality on these growth patterns were evaluated by analyzing the variance of parameters from these allometric models.

MATERIAL AND METHODS

Animals and experimental design

Data were from an experiment in which individual growth, intake, chemical body composition and organ weights were recorded in goats from birth to an age of nearly 3 years. Details of this experiment with regard to management, feed composition, recording of growth, intake and body composition were described before (Chapter 2 and 3).

Briefly, castrated male goats from the Saanen breed, a large sized European dairy breed, and the West African Dwarf (WAD) breed, one of the smallest goat breeds, were milk-fed until weaning at 9 weeks. After a transition period of 3 weeks with gradually decreasing supplementary hay, Saanen and WAD goats

(respectively groups S and DH) were offered *ad libitum* a highly digestible, pelleted feed (feed H; 10.7 MJ ME/kg DM). In a similar procedure, pelleted lucerne (feed L; 7.5 MJ ME/kg DM) was offered *ad libitum* to a second WAD group (DL).

Animals in each treatment group were randomly selected in successive age classes to be slaughtered for body analysis. Goats were taken out at birth and at ages of 2, 4, 6, 12, 18, 24 and 34 months. In this analysis only longitudinal data were used of animals that had passed the main phases of development and were in their fattening phase. This was done to minimize animal variation due to different physiological stages of growth. In a previous analysis (Chapter 2) the start of the fattening phase was estimated at 25-30% of the asymptotic weight (A) in both breeds. In this analysis animals were selected that had reached a final weight of at least 55% of A to ensure that they were in an advanced stage of fattening. This implied minimum slaughter weights of 27.5 kg for the WAD breed and 60 kg for the Saanen breed. As a result group S contained 15 animals, group DH 12 and DL 9 animals.

Measurement of body dimensions

Body dimensions of all animals were measured weekly from birth till weaning, and thereafter monthly. Liveweight (LW) was recorded weekly throughout the experiment. During measurement of chest girth and trunk length, animals were kept in a position as natural as possible. Chest girth (CG) was measured by means of a tape measure to the nearest centimetre, taking the circumference of the chest just after the forelegs. Trunk length (TL) was measured by a sliding calliper to the nearest centimetre, as the distance between the most distal positions of the major tuberosity of the humerus and the sciatic tuber. To measure the external ulna length (UL), the right foreleg of the animal was lifted first. Next, the foot limb below the carpus joint was bent fully toward the radius-ulna, and kept tight against the body in axial direction. In this position, the distance between the most distal points of the bent carpus joint and the elbow was measured by a Vernier sliding calliper to the nearest 0.1 centimetre.

Models and statistical analysis

The monophasic or simple allometric model was fitted separately to all available individual longitudinal data sets in its (natural) logarithmic form (PROC GLM; SAS, 1990):

$$\log(y) = a + b \log(x) + \underline{e} \qquad (1)$$

where y is the body dimension (mm), a the intercept, b the regression coefficient or allometric growth coefficient, x the LW (kg) and $\underline{e}$ the random error. Individual residual plots were pooled for each body dimension and group to detect systematic deviations, and underlying multiphasic patterns.

The diphasic model was based on a general multiphasic linear regression model proposed by Koops and Grossman (1993). In the analysis the following form was used:

$$\log(y) = a_1 + b_1 \log(x) - (b_1 - b_2)\, r \log[1 + e^{\{\log(x)-c\}/r}] + \underline{e} \qquad (2)$$

where y, x and $\underline{e}$ are as in (1); a_1 is the intercept, b_1 and b_2 are the regression coefficients of the two linear segments, c represents the log(x)-value in the centre of the transition zone between both segments, and r is the smoothness parameter

Parameters of the diphasic model were estimated in an iterative procedure for each animal (PROC NLIN, method DUD; SAS, 1990). There were not enough data to study accurately the exact shape of bending in the transition zone, therefore the curvature parameter r was fixed at 0.01. To avoid too large exponential values in the diphasic model, ($r \log[1 + e^{\{\log(x)-c\}/r}]$) was set to 0 for $\{\log(x)-c\}/r < -10$ or to $\{\log(x)-c\}$ for $\{\log(x)-c\}/r > 10$ as described by Koops and Grossman (1992).

To assess the improvement by multiphasic fits, the residual sum of squares (SS) and degrees of freedom were totalled in each group for both the diphasic and the monophasic model and their mean SS (MS) calculated. An F-test was applied to examine whether the diphasic MS was smaller than the monophasic

MS. Effects of breed and feed quality on model parameters were examined by two orthogonal linear contrasts (PROC GLM; SAS, 1990). The breed contrast (BR) was defined as the linear combination of treatment effects S-½DH-½DL, and the feed quality contrast (FQ) as DH-DL; F-tests were used to test whether contrasts differed significantly from zero.

RESULTS

The simple allometric model

The group means of the allometric coefficient b were similar between groups for each body dimension (Table 1). After birth, body shape changed toward a relatively larger CG ($>1/3$) and smaller TL and UL ($<1/3$), the latter showing the lowest allometric coefficient. Breed effects on parameter a for TL and UL indicate that, at equal weight, the Saanen breed is relatively longer and (assuming UL representative for total leg length) taller than the WAD breed. The breed effect on parameter a (0.152) of TL was not outweighed by a reversed small breed effect on parameter b (-0.011) over the 3.5 log units weight range. Feed quality affected parameters a and b of UL in opposite directions, and counterbalanced each other in their combined feed effect on UL.

The mean residual standard deviation (r.s.d.) was lowest in UL for all groups. Expressing these (additive) log-residuals on a non-log basis as proportional residuals, gave values of about 2% for UL, and around 3% for CG and TL (Table 1). Plots of residuals against log(LW) revealed systematic deviations from random distribution for all studied body dimensions. Dimension CG demonstrated the most simple type of systematic deviation, as illustrated for the Saanen breed in Figure 1a. Identical patterns of deviations from the monophasic fit for CG were observed in DH and DL. Also for TL (Figure 2) and UL (Figure 3) residual patterns were in general similar among groups.

Multiphasic analysis

The plots of monophasic residuals for CG pointed at a diphasic growth pattern. A diphasic model (2) was fitted, using starting values for the b_1, b_2 and c parameters which were derived from the shape of the monophasic residual

TABLE 1. *Group means and standard errors (between brackets) of parameters a, b and the residual standard deviation (r.s.d) from individual fits of the simple allometric model[1], describing growth of body dimensions relative to LW for groups S (Saanen breed, n = 15), DH (WAD breed fed H feed, n = 12), DL (WAD breed fed L feed, n = 9); significance of breed (BR) and feed quality (FQ) contrasts for both parameters*

Parameter	Group			Contrast[2]	
	S	DH	DL	BR	FQ
	Chest girth (CG)				
a	5.408 (0.009)	5.424 (0.010)	5.424 (0.012)	ns	ns
b	0.348 (0.003)	0.351 (0.003)	0.340 (0.004)	ns	ns
r.s.d	0.031	0.035	0.030		
	Trunk length (TL)				
a	5.459 (0.014)	5.309 (0.015)	5.304 (0.018)	**	ns
b	0.299 (0.004)	0.308 (0.005)	0.313 (0.006)	*	ns
r.s.d	0.031	0.033	0.029		
	Ulna length (UL)				
a	4.436 (0.010)	4.323 (0.011)	4.287 (0.012)	**	*
b	0.256 (0.003)	0.245 (0.003)	0.258 (0.004)	ns	*
r.s.d	0.021	0.018	0.020		

[1] $\log(y) = a + b\log(x)$ (natural logarithm)
[2] BR = S-½DH-½DL, FQ = DH-DL

plots. All individual data sets could be fitted without imposing boundaries to parameters during iteration, and without estimating phases based on only one or two observations at the margins of the LW range. Diphasic residuals showed no systematic deviations (Figure 1b). Estimates of b_1 were lower than those of b_2 and were homogeneous over groups, without any breed or feed quality

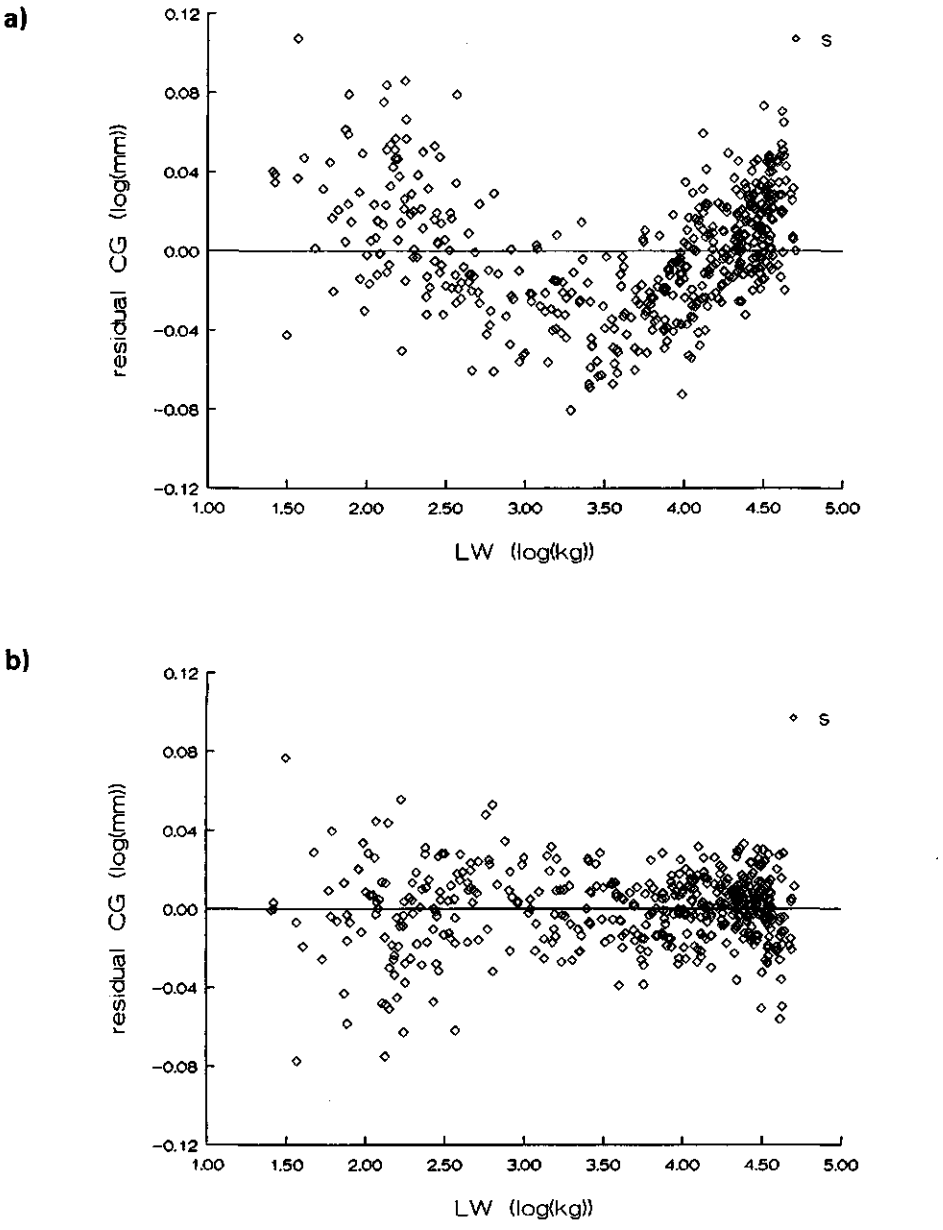

FIGURE 1. ***a)*** *Log-residuals from fits of the simple allometric model to individual data sets of chest girth (CG, in log(mm)[1)]) and liveweight (LW, in log(kg)) for 15 animals of the Saanen breed,* ***b)*** *log-residuals from fits of the multiphasic allometric model to the same data set.*

[1)] *natural logarithm*

effect (Table 2). There was a small breed effect on parameter a_1 (0.026), and a large breed effect on c (0.795). The pooled MS of the diphasic model was lower than the monophasic MS for each group (S, DH, DL; $P<0.001$).

Diphasic models were fitted to TL and UL on basis of the observed patterns in the monophasic residuals (Figure 2 and 3). Estimates for parameter c of TL were mainly located around two different weight levels in each group, whereas for some animals the model did not converge at all. Imposing boundaries on parameter c, in order to derive estimates of c from a similar part of the growth curve, resulted for some animals in estimates equal to the defined boundary. Similar problems were also encountered for UL. The diphasic model fitted data sets of most animals in DH and DL, with transition zones just after weaning, but in a few cases the model failed to converge. For the Saanen breed, estimates

TABLE 2. *Group means and standard errors (between brackets) of parameters a_1, b_1, b_2, c and the residual standard deviation (r.s.d.) from individual fits of the diphasic allometric model[1)], describing growth of chest girth relative to liveweight, for group S (Saanen breed, n = 15), DH (WAD breed fed H feed, n = 12), DL (WAD breed fed L feed, n = 9); significance of breed (BR) and feed quality (FQ) contrasts for each parameter*

Parameter	Group			Contrast[2)]	
	S	DH	DL	BR	FQ
a_1	5.504 (0.009)	5.485 (0.010)	5.471 (0.011)	*	ns
b_1	0.307 (0.003)	0.310 (0.004)	0.312 (0.004)	ns	ns
b_2	0.455 (0.013)	0.463 (0.014)	0.444 (0.016)	ns	ns
c	3.630 (0.069)	2.780 (0.078)	2.890 (0.090)	**	ns
r.s.d.	0.020	0.023	0.021		

[1)] $\log(y) = a_1 + b_1\log(x) - (b_1-b_2)\, r \log[1+e^{\{\log(x)-c\}/r}]$ (natural logarithm)

[2)] BR = S-½DH-½DL, FQ = DH-DL

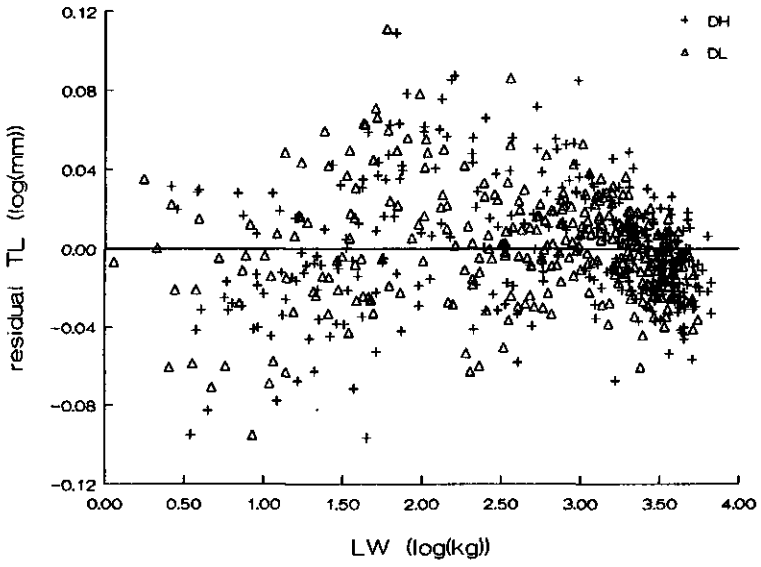

FIGURE 2. *Log-residuals from fits of the simple allometric model to individual data sets of trunk length (TL, in log(mm)[1)]) and liveweight (LW, in log(kg)) for group DH (WAD breed, fed H feed, n = 12) and group DL (WAD breed, fed L feed, n = 9).*
[1)] natural logarithm

of c, b_1 and b_2 were unacceptable as they mainly depended on the level of the chosen starting values. Also here the model did not converge for a number of animals.

The inconsistent results and fitting problems experienced for TL and UL indicate that these relative growth patterns are too complicated to be described by a diphasic model. Figures 2 and 3 suggest for both measurements a predominantly diphasic curve, which is bending after weaning (for DH and DL at log(LW) ≈ 2, and for S at log(LW) ≈ 2.7) to a decreased relative growth rate for TL and an increased rate for UL. Yet post-weaning residuals do not exhibit a fully rectilinear pattern. Both measurements show a bending zone near log(LW) ≈ 3 for DH/DL and log(LW) ≈ 3.7 for S, whereas thereafter in all groups residuals of UL show a tendency to go slightly up again until the end of the observed range.

Alternatively, a multiphasic model with more than 2 phases, could have served to account for the postweaning fluctuations. Observations in the individual data sets, however, were not frequent enough in relation to the size of random deviation, to apply such models successfully. Another approach therefore was chosen to improve the single-phased model description of TL and UL. Because all residual plots were consistent in showing a major change in relative growth just after weaning, data sets were split in a preweaning and a postweaning part, and the simple allometric model was fitted to both parts.

The split analysis showed in both breeds a strong difference between preweaning and postweaning growth of TL relative to LW, being much higher before weaning (Table 3). The absence of any effect on parameter b after weaning and the higher value of parameter a for the Saanen goats imply that after weaning this breed is longer than the WAD breed when compared at equal weight basis. The split analysis of TL gave a significantly better fit than the overall monophasic model for all groups ($P<0.01$). Contrary to TL, postweaning values of b for UL were higher than preweaning values. Breed did not affect parameter b in both parts, but parameter a was higher for the Saanen breed indicating that this breed is also longer in UL at equal weight. Comparison of the pooled MS indicated for DH and DL significant improvement of fits ($P<0.01$), but not for S ($P<0.07$).

DISCUSSION

Use of allometric models

Studies of body conformation are of biological interest as growth, functional demands during growth and body shape are closely interrelated (Brody, 1945). An accurate description of growth of body dimensions is essential for a good understanding of the relationships between shape and growth stage. The widely used simple allometric relation has clear merits, but was demonstrated here to be inadequate for a detailed description of the studied dimensions. Residuals from this model showed consistent systematic deviations in each dimension (Figure 1, 2, 3). The similarity of these patterns, despite differences in genotype and diet, indicated that fundamental growth characteristics were at the basis of these deviations and not random factors. These deviations are of particular

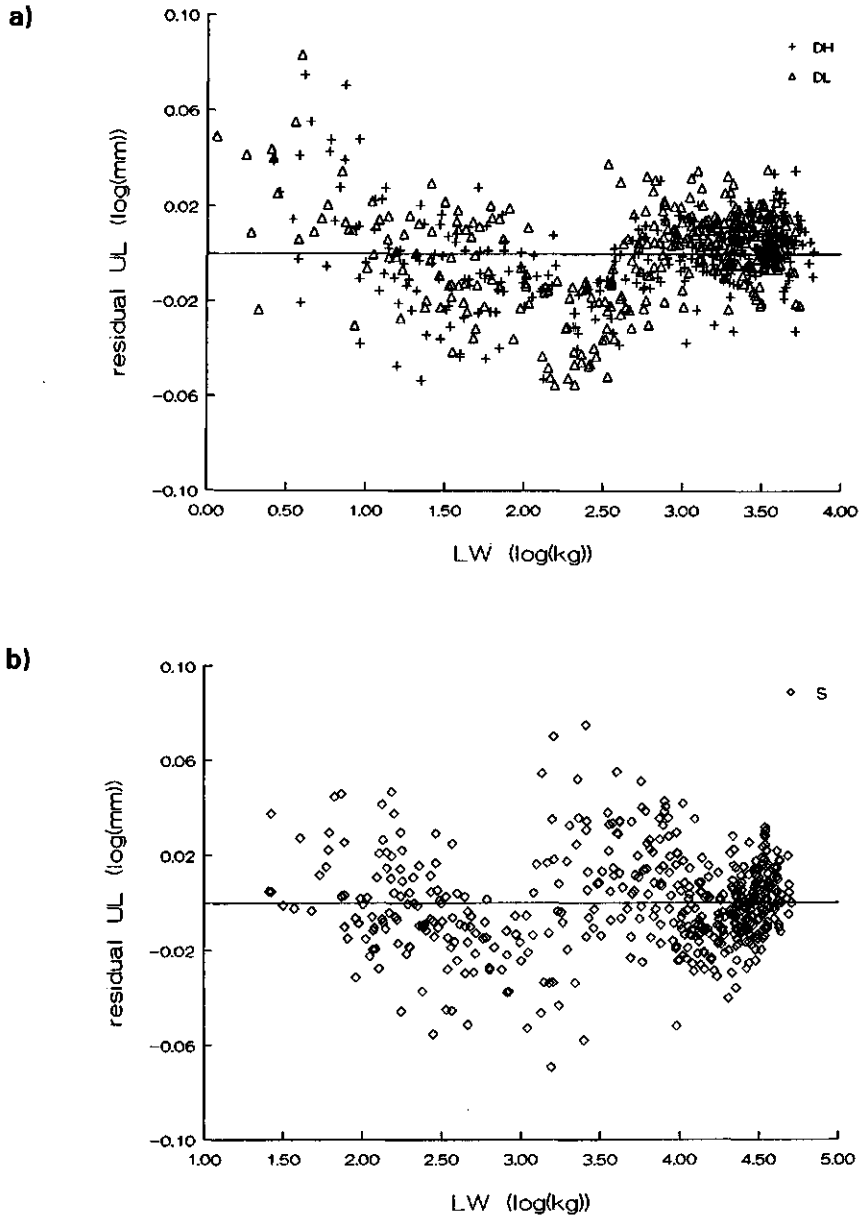

FIGURE 3. ***a)*** *Log-residuals from fits of the simple allometric model to individual data sets of ulna length (UL, in log(mm)[1)]) and liveweight (LW, in log(kg)) for group DH (WAD breed, fed H feed, n = 12) and group DL (WAD breed, fed L feed, n = 9).* ***b)*** *Log-residuals for group S (Saanen breed, n = 15).*

[1)] *natural logarithm*

interest in relation to functional demands as they reflect the changes in growth priorities. Therefore a more detailed analysis was considered to be justified.

The multiphasic allometric approach proved to give an adequate description of CG development and rendered useful information in terms of biologically interpretable parameters as discussed before in Chapter 3 and 4. The results from the split analysis for TL and UL had a more restricted biological meaning, since they merely summarize the overall allometric development before and after weaning and do not cope with some of the postweaning fluctuations. By splitting the data sets at weaning, fits for the different groups covered in most cases approximately comparable developmental stages. The final developmental level that was reached in the postweaning data set for group DL, however, stayed somewhat behind the level in group DH if expressed in terms of proportions of their asymptotic weights, though the final weight differences on log-scale are minor (Figure 2 and 3). Results with regard to postweaning effects of feed quality therefore has to be interpreted with some caution.

Growth of trunk length and ulna length

The monophasic estimates in Table 1 show a consistent overall pattern among the groups. After birth, body trunk dimensions developed relatively stronger than leg lengths. Brody (1945) found the same for cattle. Searle et al. (1989a) estimated b values in wether sheep (Leicester x Merino) which were fed *ad libitum* or ½ *ad libitum* of 0.26 and 0.32 respectively for body length, and 0.15 and 0.23 for leg length. In a subsequent study Searle et al. (1989b) estimated b values in *ad libitum* fed Corriedale and Dorset Horn sheep of 0.338 and 0.298 respectively for body length, and 0.191 and 0.161 for leg length. These rankings of b values are confirmed in this study.

Dimensions TL and UL could not be described adequately by a multiphasic model, but splitting at weaning improved fits considerably in most cases. The choice of weaning as breaking point was based on the pronounced change in monophasic residuals just after weaning. Apparently the strong physiological changes, accompanying the transition in feed type, also had an impact on the growth of TL and UL. Individual plots showed that most animals, especially in DL, were retarded in UL and TL growth just after weaning. The strong

TABLE 3. *Group means and standard errors (between brackets) of parameters a,b and residual standard deviations (r.s.d.) from individual fits of the simple allometric model[1], describing separately preweaning and postweaning growth of Trunk length and Ulna length relative to liveweight, for group S (Saanen breed, n = 15), DH (WAD breed fed H feed, n = 12) and DL (WAD breed fed L feed, n = 9); significance of breed (BR) and feed quality (FQ) contrasts for each parameter*

Parameter	Group			Contrast[2]	
	S	DH[3]	DL[3]	BR	FQ
	Trunk length (preweaning)				
a	5.259 (0.020)	5.228 (0.017)	-	ns	-
b	0.390 (0.013)	0.364 (0.011)	-	ns	-
r.s.d.	0.037	0.0293	-		
	Trunk length (postweaning)				
a	5.529 (0.015)	5.383 (0.017)	5.364 (0.019)	**	ns
b	0.281 (0.004)	0.285 (0.005)	0.294 (0.006)	ns	ns
r.s.d.	0.020	0.025	0.021		
	Ulna length (preweaning)				
a	4.503 (0.017)	4.337 (0.014)	-	**	-
b	0.226 (0.009)	0.228 (0.008)	-	ns	-
r.s.d.	0.018	0.016	-		
	Ulna length (postweaning)				
a	4.431 (0.018)	4.278 (0.021)	4.225 (0.024)	**	ns
b	0.258 (0.005)	0.259 (0.006)	0.278 (0.006)	ns	*
r.s.d	0.020	0.012	0.015		

[1] $\log(y) = a + b\log(x)$ (natural logarithm)
[2] BR = S - ½DH - ½DL, FQ = DH - DL
[3] Parameters of DH and DL were combined for the preweaning datasets

development of the forestomachs at this growth stage (Chapter 4) might have changed growth priorities between components. This retardation, however, could also have been partially caused by expanding gut fill just after weaning, which was especially pronounced in the low feed quality group DL (Chapter 3). A straightforward diphasic analysis of TL and UL was probably obstructed by this retarding effect just after weaning and by fluctuations in the relative growth gradient in the final part of the observed range.

Growth of chest girth

Growth of CG relative to LW showed a diphasic pattern in all groups, groups having equal b values within each phase. This consistency for parameter b points at a similar physiological basis for the diphasic pattern in both breeds. The proportional enlargening of CG in the second phase might be related to the fat growth pattern. Earlier analysis of chemical composition in these animals (Chapter 3) demonstrated a diphasic pattern of fat growth relative to fatfree weight, with an increased rate of deposition in the second phase. The empty body weight (EBW) levels at which fat growth accelerated were estimated at 25.5, 11.1, 12.3 kg for S, DH and DL respectively. These levels were somewhat lower than the transition levels of 32.4, 14.3 and 14.8 kg EBW for CG in this study, using estimates for LW from Table 2 and equations from Chapter 3 to convert LW in EBW. An explanation could be that fat is first deposited in internal fat depots, like omental and kidney fat. After completion of these depots, fat is directed toward muscular and subcutaneous fat layers, which on their turn cause a disproportional increase in CG.

Epiphyseal closure

Description of postweaning growth of TL and UL by one allometric coefficient masked some subtle, but remarkable growth features. Residual patterns in Figure 3 clearly demonstrate a higher growth gradient for UL after weaning, followed by a decreasing trend. Surprisingly, this trend is reversed in the final part (especially well noticeable in Figure 3b). The prepubertal growth of the long bones is induced by sex hormones, and the increased concentration of these hormones during puberty stimulates epiphyseal closure, resulting in a cessation of bone length growth (Short, 1980). This process of epiphyseal closure is retarded in animals that are castrated before puberty (as animals in this study

were), which must lead to animals that are taller compared to intact animals of similar weight. Robertson et al. (1970) demonstrated this phenomenon in cattle. The goat data in this study indicate that no epiphyseal closure took place at all, as UL continued to grow relative to LW. The increasing trend at the end of the observation range even suggests that bone length continues to grow autonomously at a constant rate in time against a decreasing rate in total body growth.

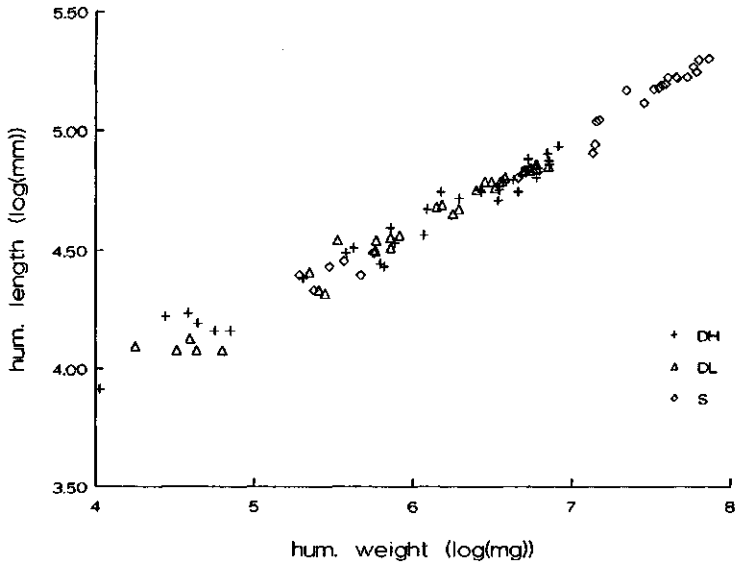

FIGURE 4. *Development of humerus length relative to humerus weight, based on cross-sectional slaughtering data of group S (Saanen breed, n = 15), DH (WAD breed, fed H feed, n = 12) and DL (WAD breed, fed L feed, n = 9).*

Cross-sectional slaughtering data from the same animals are in line with the presumed absence of epiphyseal closure in long bones. From birth to maturity, data on humerus weight and length were collected as described earlier (Chapter 4). Figure 4 shows the simple allometric relationship between humerus length and weight, with no signs of diminishing length growth at heavier bone weights, as might have been expected in case of epiphyseal closure. These results imply that adult (or asymptotic) values of bone dimensions are

inappropriate indicators of genetic size. They lead to different values for castrated and entire animals. Related traits like adult ash weight (Kyriazakis and Emmans, 1992) are also questionable for the same reason.

Comparison of body shape between genotypes

The split analysis showed that the Saanen breed were longer in TL and UL than the WAD breed; postweaning parameters indicated, at equal weight basis, a larger size of 15-20% for both dimensions of the Saanen breed. These differences, however, may not be interpreted as evidence for breed differences in body shape, since developmental differences are also involved in such a comparison. Comparison at equal weight of breeds that differ in genetic size implies that animals are compared at different degrees of maturity. At the same weight the genetically larger Saanen breed is at a lower degree of maturity than WAD goats of the same weight. Because TL and UL have b values smaller than 1/3, indicating a proportional decrease in TL and UL during maturation, the Saanen breed must have a longer TL and UL at equal weight. On the contrary, absence of any breed differences at similar weight for these dimensions would have indicated breed differences in body shape.

Some authors claim that the dwarf characteristics of the WAD breed can be attributed to achondroplasia (Mason, 1984). In such a case a disproportional low ratio of UL/TL is expected for dwarfs, as achondroplasia mainly affects development of the long bone lengths and not trunk length. As outlined before, ratios of UL/TL should not be compared at equal weight but at equal degree of maturity. If we take equal proportions of asymptotic weight (parameter A in Table 4 of Chapter 2) as a basis for comparison, corresponding ratios of both breeds may be compared to assess whether UL/TL ratios are smaller for WAD goats. Ratios for three developmental stages of group S and group DH were calculated which cover the observational range: 0.04A, 0.25A and 0.75A. Using the equations from Table 3, ratios at the subsequent proportional levels of A for group S and DH were, 0.37 and 0.37, 0.34 and 0.31, 0.30 and 0.30 respectively. Ratios decline since UL has lower b values than TL for both breeds. There is no sign of systematically lower ratios for the WAD breed. The overall picture is that ratios are fairly similar, implying similar developments in body shape with respect to the ratio of these two dimensions. Hence, these

results do not lend any support to achondroplasia as a physiological basis for dwarfing of the WAD breed.

Hall (1991) compared body dimensions of adult WAD goats and sheep from the south of Nigeria to larger bodied breeds from the north. He concluded that the WAD goats were a proportional miniaturization of the northern breed, whereas the WAD sheep were a neotenous form of northern sheep (i.e. adult WAD sheep showed juvenile characteristics of the northern breed). He based these comparisons, however, on ratios of body measurements to LW, without correcting for the difference in dimension. This inevitably leads to a distorted picture as such ratios become higher in case of scaling down to similar shaped, smaller sized mature animals; conclusions based on such ratios are therefore not valid. Recalculation of these ratios by using the cube root of LW demonstrated a different pattern. Both adult WAD sheep and goats were relatively shorter in withers height and body length than their northern counterparts. These ratios suggest, contrary to Hall's conclusions, that breed adaptations of body shape to different ecological zones were similar in both species.

Genetic size

The breed effect on parameter c of CG reflects a difference in body size at a corresponding stage of growth and might therefore be used as a measurement of genetic size. At this transition stage, the Saanen breed is 2.23 times heavier than the combined groups DH and DL. This ratio lies close to values of 2.16 for asymptotic LW, 2.20 for asymptotic EBW and 2.18 for the onset of the second phase of fat growth which can be calculated from estimates in Chapter 2 and 3. These ratios show a close agreement between estimates based on allometric growth patterns (fat and CG) and asymptotic values derived from age-weight relations (LW and EBW).

Allometric growth patterns offer a practical and promising alternative to age-weight relations for determination of genetic size, because these patterns can be established during early phases of growth, and are not easily altered by environment. Feed quality did hardly affect growth patterns of the dimensions in this study; only postweaning growth of UL was affected, but to a minor

extent as effects on parameters a and b counterbalanced each other. Longitudinal observations of body dimensions offer an additional advantage over cross-sectional data for genetic size determination, as they allow for individual estimates of size. In this study individual asymptotic standard errors of c estimates for CG were relatively large compared to the within-breed individual variance of parameter c. It should be possible, however, to increase accuracy by more frequent measuring in the weight range where transitions in multiphasic growth patterns may be expected.

Conclusions

In conclusion, multiphasic analysis described growth of CG relative to LW better than a monophasic approach. The observed breed effects on the identified transition zones in CG might serve as indicators of genetic size. Feed quality did not affect growth of CG. Although the data sets of TL and UL could not be fitted adequately by a multiphasic model, separate analyses of preweaning and postweaning growth improved their description. Comparison of TL/UL ratios at different degrees of maturity indicated no major breed differences, indicating that the dwarf characteristics of the WAD breed were not due to achondroplasia. Monophasic residuals of UL after weaning showed systematic changes in relative growth patterns, and indicated the absence of epiphyseal closure in these castrated animals. This phenomenon casts doubt on the appropriateness of asymptotic values of bone dimensions of castrated animals as measures of genetic size.

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CHAPTER 6

EVALUATION OF GENETIC SIZE MEASURES

ABSTRACT

In this final section the results and conclusions of the foregoing chapters are integrated to evaluate genetic size measures that are accurate and practical in use. Different types of genetic size characteristics and their measures are presented, and classified according to different selection methods for size measures. These measures are assessed on basis of criteria outlined in Chapter 1. Three groups are distinguished: measures related to major functional changes, measures based on size-age relationships, and measures based on characteristics of allometric growth patterns. Measures from the first group, like birth and sexual maturation do not offer perspectives for improvement in size determination. In the second group, possible measures are discussed separately for weight-age relations and body component-age relations. Asymptotic weight (WA) is not a suitable measure to describe genetic size of animals in normal animal production environments. The experimental results supported the use of WA as genetic size measure under controlled conditions. Multiphasic analysis of weight-age relations may yield genetic size measures only where full controll of all environmental factors is possible. Among body component-age relations, in particular bone lengths offer perspectives; mature bone lengths or characteristics from multiphasic analysis could be applied. Both simple allometry and multiphasic allometry provide information on genetic size. It is explained how the phenomenon of allometric transposition is related to genetic size differences. Transition zones in multiphasic allometry can be used as genetic size indicators. Multiphasic allometry in chest girth offers a possibility to determine genetic size from an external measure. In the final section it was concluded that, although limited in number, some measures offer perspectives for improvements that enable a better use of the genetic size-scaling theory. Prospects for use of genetic size measures at production level and experimental level are discussed.

EVALUATION OF GENETIC SIZE MEASURES

INTRODUCTION

Understanding of scaling processes is of great interest in explaining genotypical variation in biology. Within the main taxonomic groups, a considerable part of the variation across genotypes can be explained by scaling phenomena. The genetic size scaling theory (Taylor, 1985) provides a set of scaling rules and a scaling factor, based on genetic size, by which differences in scale between genotypes can be quantified. The usefullness of this theory for animal production depends to a large extent on its ability to explain genotype variation between individuals or between groups of individuals within species. So far, its implementation has been mainly hampered by lack of a suitable practical method for size determination (Chapter 1). The objectives of this study, as outlined in the introductory chapter, were formulated in view of these implementational problems. The first objective of this thesis was to explore measures for genetic size that were practical and accurate, and the second aimed at elaborating methods for genotype evaluation of growth characteristics which incorporate the genetic size concept.

In this final section the results and conclusions of the foregoing chapters are integrated in view of the central objectives. First, different types of genetic size characteristics and their measures are presented, and classified according to different selection methods for size measures. Characteristics of genetic size observed in this study are discussed. Measures of these different characteristics of genetic size will be compared with the size of the fatfree component of asymptotic weight, which is taken here as a reference measure for genetic size. Their suitability as practical measures is judged on basis of the criteria outlined in Chapter 1. Finally, the conclusions of the preceding sections are used to discuss implications and prospects for use of genetic size measures in different types of genotype evaluation.

CLASSIFICATION OF MEASURES AND CRITERIA FOR ASSESSMENT

Classification and measures of genetic size characteristics

The genetic size factor is expressed at all developmental stages of growth (Taylor, 1985; Chapter 1), and therefore can be characterized and quantified in numerous ways. It is evident that any description and quantification of genetic size of a number of genotypes should be based on equivalent developmental stages. Consequently, the number of genetic size characteristics that can be identified is depending on the number of specific equivalent stages of development that can be identified.

Genetic size characteristics may be classified according to groups of developmental stages. Developmental stages can be described by either direct observation of functional changes or by identifying characteristics of relationships between growth variables. These characteristics should refer to a specific stage of physiological development. The following groups of developmental stages are distinguished:

1. Stages that are characterized by externally observable switches in physiological functioning; for example birth, first oestrus signs, start of laying period in birds.
2. Stages that can be defined on basis of size-age relationships, like the full maturity stage that represents the final condition of no further change. Similarly we might also define a stage related to maximum change of size in time.
3. Stages related to characteristic changes in relative growth patterns which are linked to functional development. An immediate change in the ratio of the relative growth rates of two components might serve as an indicator for such stages, like the onset of the second phase of fat growth relative to fatfree growth.
4. Stages related to a specific ratio between two components. Ratios of components are preferred that are known to correlate strongly with physiological development; for example a certain percentage of water in fatfree weight could be taken as reference basis for genetic size, since this percentage decreases during maturation. Although sometimes the

direct functional relation of a given ratio to total physiological development might not be directly clear, such ratios can be interpreted as indirect indicators of development because of their correlation with overall physiological development.

This classification of groups of genetic size characteristics is not intended to be complete. Groups can be added that refer to other markers of physiological development, like particular hormonal or morphological changes. The groups listed before are based on weight and time variables that are commonly measured in growth studies and demonstrate that even on basis of such a restricted group of variables, in principle, many approaches can be followed to find suitable genetic size characteristics.

Once a particular developmental stage has been identified as reference basis, genetic size has to be quantified, i.e. has to be expressed by a measure. Depending on how developmental stage is defined, several measures can be useful. In cases where genetic size determination is based on developmental stages that are not linked to a particular component (group 1), weight of the total body or weight of certain components (like fatfree weight) can be taken as a measure.

If characteristics refer to a developmental stage of a particular component, then genetic size can be quantified either *directly* by the size of this component or *indirectly* by the size of other components at this stage. For example size determination based on the onset of a new growth phase of fat (group 3) can be both measured by the weight of the component itself as by total body weight at this onset.

Selection methods for genetic size measures

Starting from the foregoing classification of size characteristics several approaches can be followed to select measures for genetic size:

I Identification of major functional changes that are externally observable.

II Deriving genetic size characteristics from size-age relationships of total body and body components. Relevant measures can be obtained from describing these relationships by appropriate growth models. The most common and straightforward approach is to use the asymptotic weight parameter of classic growth models, like the logistic model or the Gompertz model (Fitzhugh, 1976). Another option is to examine the existence of multiphasic growth patterns by multiphasic growth functions (Koops, 1989), and, if appropriate, base size on the asymptote of an underlying growth phase.

III Examination of allometric growth patterns of body components. Both multiphasic patterns, as indicated before in the third group of size characteristics, and simple allometric patterns are of interest.

In this thesis a number of relationships was studied from which genetic size characteristics and related measures could be derived. The majority of these measures were obtained from allometric growth patterns, but also other types of measures could be selected. In the next sections these measures, grouped according to selection method, will be discussed in view of criteria listed below.

Criteria for practical and accurate genetic size measures

In Chapter 1 of this thesis a number of conditions were formulated for a measure of genetic size to be accurate and practical in use; for ease of reference they are repeated here once more:

1. The measure should explain as much as possible inter-specific and intra-specific variation of cumulative, rate and time variables at any stage of development.
2. It should correspond to a clearly identifiable, equal stage of development.
3. It should be independent of the animal's nutritional and environmental history.
4. It should be determined at a developmental stage that lies within the normal weight range of farm animals, preferably as early as possible.
5. It should be a simple external measurement, easy to measure *in vivo*.

These conditions will be used as criteria for evaluation of groups of genetic size measures from this study. In addition, size measures will be compared with a reference measure for genetic size which is accepted as an accurate genetic size measure. For reasons discussed in Chapter 3, the size of the fatfree component of asymptotic weight (FFWA) is taken as reference measure.

The reference values of FFWA were calculated on basis of the group means of asymptotic liveweight (LW) for the three experimental groups (parameter A, Chapter 2, Table 4). These means were corrected for gut fill, using the allometric equations describing empty body weight (EBW) as a function of LW (Chapter 3); the fatfree component in EBW was calculated from the diphasic relation between fat and fatfree (Chapter 3), being the amount of fatfree tissue at which the sum of fat and fatfree corresponded to the estimated values of EBW. According to this procedure the values of FFWA for the Saanen goats (S) and the WAD goats of group DH and DL were: 50.0, 23.8, 23.7 kg respectively; the breed ratio (S:DH) for FFWA was 2.10.

EVALUATION OF GENETIC SIZE MEASURES

Measures based on major functional changes

Major functional changes in life of mammals are taking place at birth, weaning, and the onset of puberty. The occurrence of weaning in the experiment was imposed by management, and is known in farm animals to be, in general, highly dependent on management. Although especially in ruminants weaning involves physiological changes, this stage provides no suitable basis, because the environmental component obstructs a clear expression of genetic factors. In free living animals, weaning is a more gradual process, but still subject to environmental factors. Gradual changes, however, are not very suitable in this respect as they do not correspond to a definite developmental level.

Sexual development

The transitional phase in a young immature animal toward sexual maturity is characterized by a number of subsequent developmental changes of which some might serve as reference basis for genetic size determination. In female

mammals, for instance, characteristic landmarks in sexual development are the onset of cyclic hormonal patterns related to first ovulation, and first external signs of oestrus behaviour. In males, phasic patterns in gonadal development and the first signs of typical behaviour related to sexual maturity could be used as developmental landmarks. It is well established, however, that breeding in many species is regulated by seasonal factors like daylength. Domestic sheep, goats and horses from temperate zones are known to have seasonal breeding rhythms (Brody, 1945). Yet, many species evolved in the tropics do not respond to seasonal light patterns. This different behaviour is exemplified by the two goat breeds in the experiment. The temperate Saanen breed normally has a limited breeding season in the autumn, whereas the WAD goats can be bred throughout the year. Such breed differences complicate measures of genetic size based on first signs of sexual development.

In the experiment, no measure related to sexual development could be derived since the experimental male animals were castrated a few weeks after birth. Castration uses to be part of the standard management procedures of the goat experimental unit where the animals were kept, because large numbers of castrated animals are much easier to keep than bucks. In this trial, for the same reasons similar procedures were followed, as well as for reasons of being able to compare feed intake and growth performance with the large amount of results from previous trials with WAD goats. The absence of sexual development, however, appeared to have much more profound effects on development, in particular on bone development (Chapter 4), than was anticipated. As will be discussed hereafter in relation to body dimension measures, possibly useful stages in bone growth could not be studied. In retrospect, it is believed here that studying intact animals would have provided more information and should be preferred in studies that aim at identifying clearly observable developmental stages.

Birth

Birth represents a distinct developmental stage, that within-species corresponds to an equivalent functional stage. Birth weight (BW) therefore might seem attractive as a possible genetic size indicator, as it matches convincingly the size measure conditions 2, 4 and 5. However, BW is known to be strongly

influenced by a number of non-genetic factors (condition 3) like parity number and litter size. Analysis of variance of BW based on the herd groups from which the experimental animals were derived showed that litter size and parity number explained 46% of total BW variation of the Saanen group and 28% in case of the WAD goats (analysis not included in this thesis). In principle, individual BW could be adjusted for these two factors if such relationships are known, but this requires extra information in practice. Correction is also needed for maternal genetic size. BW is affected by the prenatal nutritional level which is likely to be positively correlated with maternal size. This effect biases individual estimates of BW in the direction of maternal size. Particular in crossbreeding of very differently sized breeds such effects can be considerable, as shown in studies on crossbreeding differently sized horse breeds (Walton and Hammond (1938), cited by Hammond (1940)), and on crossbreeding small Vietnamese pigs with large-sized Landrace pigs (Thikonov and Ratiani, 1974).

The use of BW as size measure is further complicated by two other factors: an almost fixed gestation length within-species, and breed variation in litter size. Taylor and Murray (1987) examined inter-breed relationships in cattle and concluded that BW/littermass is proportional with dam weight to the power 0.83. Donald and Russel (1970) found in sheep that at equal litter size, BW was proportional to the power 0.73 of maternal weight; this power is according to Taylor and Murray (1987) somewhat higher in case of mean litter mass. It is likely that these scaling effects are related to the nearly fixed gestation length within species. This scaling effect obstructs a straightforward use of BW as genetic size measure. Another question to be solved is how to deal with intra-specific and inter-specific differences in litter size, which can be quite considerable in some ruminant species. At breed level one might solve this problem by taking the averaged total litter mass of a group of animals to characterize breed size, but this procedure has no value for evaluation of individual genetic size within groups.

Total litter mass (males and females) recorded in the experimental herd groups amounted 7.24 kg for Saanen goats and 2.86 kg for the WAD goats (breed ratio 2.53). When corrected for the on average higher parity number in Saanen goats, litter mass was respectively 6.74 and 3.16 kg, giving a breed ratio of

2.13, which is close to the value of 2.10 for FFWA (because the fat percentages at birth were practically the same in both breeds, the ratio for BW is not changed when expressed on fatfree basis). If the inter-breed relationships between litter mass and maternal weight also account for goat breeds, a lower value would have been expected of around $2.10^{0.73 \text{ to } 0.83} = (1.72 \text{ to } 1.85)$. The higher observed ratio is in line with the higher than expected postnatal growth rate in the Saanen breed (Chapter 2), keeping both breeds at equal proportions of their asymptotic weight at the same chronological age. Having the same gestation length and therefore being at the same age at birth, the same apparently occurred for prenatal growth. The example illustrates how this higher than expected growth rate of S undermines estimates of genetic size based on litter mass if corrected for inter-breed scaling effects.

In conclusion, weight at birth or related measures like litter mass are not acceptable practical measures for genetic size in view of the forementioned considerations; a number of corrections are needed that require much extra information. Even if corrected for environmental factors, the experiment shows how other effects, that are probably due to differences in metabolic rate, may change breed ratios considerably.

Measures based on size-age relationships

Genetic size measures may be based on common characteristics of size-age relationships. Among size-age relationships, liveweight-age (W-t) relations are most frequently recorded in experiments, and it seems therefore appropriate to start assessment of possible genetic size characteristics from this relationship. This will be followed by a discussion of possible measures based on relationships between age and specific parts of the body, in particular bone length.

Maximum growth rate

An often mentioned characteristic of the W-t relation, besides asymptotic weight, is the weight or age level at which maximum growth occurs. In growth functions, maximum growth occurs at the point of inflection. The point of inflection is generally associated with the onset of puberty (Brody, 1945). In practice, it is a difficult task to locate the exact weight level corresponding to

maximum growth. One reason for this can be easily understood from the normal shape of weight curves. The common pattern is that growth rate is almost constant in an extended part of the weight curve centred around the maximum growth stage, from which it is difficult to estimate accurately the exact stage at which growth rate is maximal. One may prefer to base determination on applying one of the many growth models, but here the choice of model has a strong impact on the estimate, since in many models inflection points have a fixed relationship with the asymptote.

Another disadvantage of maximum growth is that its occurrence not necessarily linked to a specific developmental stage like puberty, since nutritional factors may modify to a considerable extent the shape of the weight curve. Restriction in feed at varying ages may result in different shapes, but also in *ad libitum* fed animals changes in feed quality alter growth curves. This was demonstrated in the experiment within the WAD breed; Figure 2 of Chapter 2 shows how the shape of weight curves differed for both feed qualities. In ruminant species, maximum growth lies close to weaning. Variation in weaning age and feed quality during this period therefore could have an important effect on the weight level associated with maximum growth. Hence it is concluded that the use of the maximal growth characteristic as a basis for size determination does not offer any perspective for improvement in determination of genetic size.

Asymptotic weight

Asymptotic weight (WA) plays an important role as genetic size measure in many genotype comparisons that include genetic size concepts. Normally determination of WA is based on W-t data. In the analysis of this experiment WA was also used as a genetic size measure, but was estimated from the relation between weight and cumulative feed intake according to the method of Parks (1982). Cumulative feed intake seems to be the only input variable that is of interest in quantifying genetic size, but in case of ruminants is only very occasionally measured for the main part of the growth curve due to practical restrictions. Park's approach of estimating WA has the advantage that results are less easily disturbed by random factors affecting intake and growth than estimates based on W-t data. From a practical point of view, however, WA is

more simply determined on basis of W-t data, where no recording of feed intake is required.

Practical and theoretical limitations of WA as genetic size measure were adressed in Chapter 1. These limitations will be discussed here in relation to experiences in this experiment. The serial slaughtering design of the experiment limited to a considerable extent the number of animals from which sufficient data could be collected for reliable, stable estimates of WA. The equilibrium weights of animals that have free access to good quality feeds, appeared to be substantially higher than those normally observed in the flocks of breeding animals, which for both breeds are weighing about 50-60% of WA. Consequently, the experimental animals had to be followed over a relatively much longer weight range than would be expected from equilibrium weights of breeding animals. Growth experiments of this type, therefore, tend to be laborious, time-consuming and expensive, even in case of relatively small ruminant species like goats.

Another important practical limitation of WA arises from the different equilibrium levels of experimental and breeding animals. This difference is likely to be due to both physiological and management factors. Contrary to the experimental animals, breeding animals are part of the time pregnant and/or lactating, and breeding animals on farms are never continuously *ad libitum* fed with pelleted feeds but are subjected to a much more restricted feeding regime. The equilibrium levels of breeding animals therefore are of limited use as genetic size measure, because they are considerably affected by a number of non-genetic factors. Consequently, weight data of normal farm animals cannot provide a proper basis for measures of genetic size in cases that demand a high accuracy of size determination like individual comparisons or comparisons of breeds that differ only slightly in size. If WA is to be successfully used as genetic size measure, accurate estimates are required that can only be obtained under controlled management conditions, i.e. under experimental conditions.

Earlier in Chapter 1 it was questioned whether the huge quantities of fat deposition during the final growth stages reflected the genetic size factor of earlier growth. It is possible that large genetic differences exist between

individuals, breeds and species in their ability to deposit fat. Indeed, the experimental goats reached extreme fat levels when approaching maximum weight, in accordance with observations in a long term growth trial with *ad libitum* fed wether sheep (Blaxter *et al.*, 1982). The results showed that at least among the two studied breeds the estimated maximal fat depositions seemed to be in reasonable agreement with their differences in genetic size as expressed by FFWA. Using the equations from Chapter 3, the fat levels of maximum empty body weight were estimated at 49% in the Saanen breed and 47% in the WAD breed. Blaxter *et al.* (1982) found a slightly higher level of 54% in wether sheep (maximum weight 120 kg EBW). These fat levels are of the same order of magnitude and do not suggest large breed/species differences, as such they do not undermine the use of genetic size measures like WA that include the fat component. This is also illustrated by the fair agreement in breed ratios of FFWA and WA, being 2.10 and 2.19 respectively.

In the experiment feed quality did not alter levels of WA. The same was found by Blaxter *et al.* (1982) in wether sheep for two pelleted feeds that differed in ME contents in dry matter. These findings do not exclude the possibility that feed quality may alter WA levels. In fact there is a group of feeds with a very low quality on which *ad libitum* fed animals lose weight, and never reach WA. On natural grasslands, ruminants alternately lose and gain weight because of seasonal changes in feed quality, and never reach maximum weight levels because of these fluctuations. Restricting to feed qualities on which positive growth rates can be obtained, the question remains whether animals reach the same maximum weight irrespective of quality. If not, WA is a less adequate measure of genetic size, but so far there is no evidence that suggests any effect of feed quality on WA in ruminants.

In conclusion, WA is not a suitable practical measure to describe genetic size of animals in normal animal production environments. Controlled conditions are required to exclude management effects on WA. The absence of effects of feed quality on WA and the absence of substantial differences in fat levels between breeds, observed in this experiment, support the use of WA as a genetic size measure when applied under controlled conditions.

Multiphasic analysis of W-t relationships

Multiphasic growth functions have been successfully applied and are widely accepted in the analysis of human size-age relationships (Tanner, 1977). Koops (1989) investigated the use of multiphasic growth functions in animal growth and demonstrated that W-t data of rats, mice and rabbits were better described by multiphasic functions than monophasic ones. He concluded that application of multiphasic growth curves improved the insight in growth patterns of body weight or other size measures, and concluded that multiphasic functions can contribute to determination of stages of physiological development. This means that this type of analysis might be useful in determination of genetic size. From multiphasic analysis asymptotes and maximum growth stages can be derived and be used as size measure. This offers possibilities for determining genetic size at an earlier stage of growth than full maturity.

Multiphasic growth functions can be used in cases where both systematic environmental factors and internal factors affect growth. If environmental factors, however, behave non-systematically and if many of them act at the same time, results from multiphasic analysis are not interpretable. In such cases, it becomes extremely difficult to distinguish internal factors from environmental ones. In small experimental animals, like mice and rabbits, it is usually possible to have full control of their environment and keep all environmental factors constant. If required, the effects of restricted numbers of external factors on these small animals can be studied by multiphasic analysis.

For a number of reasons, control of environment is more complicated in case of the much larger ruminant species. For these animals it is difficult and costly to keep factors like feed quality and temperature exactly the same during their much longer growth period to maturity. Effects of feed type changes around weaning, of seasonality and of small disturbances due to occasional diseases add up to the forementioned effects. In long term growth experiments with sheep (Blaxter *et al.*, 1982) and goats (Ketelaars and Tolkamp, 1991), these types of uncontrolled factors complicated interpretation of results. A number of these factors also played a role in this experiment (Chapter 2). Although they did not disturb the overall growth patterns of the treatment groups, their

combined effects on parts of the growth curve obstructed a meaningful multiphasic analysis of size-age data in this experiment.

It is concluded here that, only where full control of all environmental factors is possible, multiphasic analysis can be useful and offers options for genetic size measures. This appears to be complicated in experiments with ruminant species. Genetic size measures derived from multiphasic analysis of W-t data are not applicable in ruminants, unless it is demonstrated that environmental factors can be much more restricted in long term experiments with ruminants than has been shown so far.

Measures based on body components

Size-age relationships of body components may be of more interest than W-t relations for two reasons:

1. Growth curves of particular body components may be less affected by environmental factors than full liveweight. If the shape of their growth curves are well established, asymptotes of such components can be estimated at an earlier growth stage and with more accuracy than relatively unstable components. In such components multiphasic growth patterns, if existing, are easier detected and can be analyzed with higher accuracy.

2. Components may attain full maturity earlier than full weight, which reaches full maturity only after all body components have done so. Reaching early full maturity offers an important practical advantage for size determination.

The genetic size measure FFWA, which is used in this chapter as a reference measure, is regarded by many to be a better genetic size measure than asymptotic liveweight (A), because development of the fat component is considered to be more dependent of nutritional factors than the fatfree part. Especially in monogastrics, nutritional factors are known to have profound effects on body composition. In ruminants, body composition is less easily manipulated by nutritional environment (Theriez *et al.*, 1982). In this

experiment, for example, no effects of feed quality on the relation between the major chemical body components were observed (Chapter 3).

Many body components may be distinguished, besides the fatfree component, that are of interest for size determination. For practical reasons, however, components are to be preferred whose size can be determined externally by simple methods. This limits possible measures mainly to lengths of externally measurable long bones. Bone length measures generally have a more stable character than body mass. Diseases and changes in feed quality may affect weight development considerably as a result of instantaneous gut fill changes and losses in EBW, whereas bone lengths eventually may stop growing but do not decrease. In human biology, stature length is widely accepted as a stable measure for describing development from birth to adulthood (Tanner, 1977). The best and simplest bone characteristic that can be used as genetic size measure is the bone length at full maturity. Bone lengths mature earlier than the fat component and remain stable in length due to epiphyseal closure, which takes place during sexual maturation (Short, 1980).

The long term growth study of Wiener and Hayter (1974) on body growth and development of body dimensions in ewes of five sheep breeds and their crosses provides and example of the early maturation characteristics of bone length. Their results show that tibia and cannon bone length reach their final size before the animals are one year old and remain stable thereafter, whereas body weight still continues to increase after the second lambing in three-year-old ewes (Figure 1). Body dimension measures studied in this thesis, however, showed no signs of earlier maturation relative to body weight. This is demonstrated in Figure 2 for Saanen goats whose body dimensions were recorded during the full experimental period; their development of ulna length is plotted against both age and weight and shows no plateau. It was concluded in Chapter 5 that epiphyseal closure in experimental animals did not occur, apparently as a result of early castration. Therefore no attempt was made in this study to quantify genetic size on basis of mature bone lengths.

Although no direct comparison was made in this study between castrated and intact animals, the maximum body frame size of castrated animals has to be

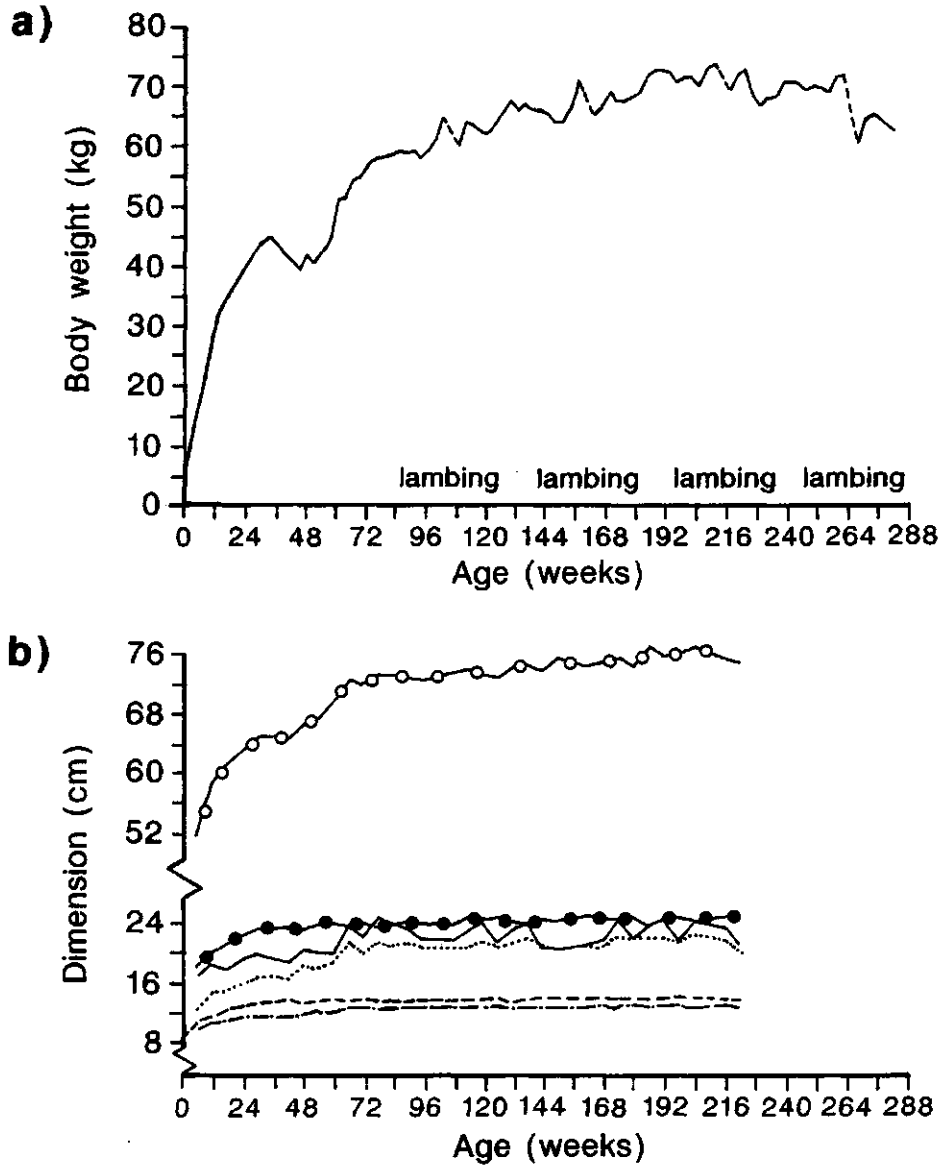


FIGURE 1. *a) Growth of body weight (kg) versus age (weeks), from birth to 5½ years, of Scottish Blackface female sheep, b) development of 6 linear dimensions (cm) against age, from 6 weeks to 4½ years, of the same sheep; linear dimensions: body length o—o , shoulder width —— , hook width ····· , head width —·—·— , tibia length ●—● , cannon bone length - - - - - , from Wiener and Hayter (1974).*

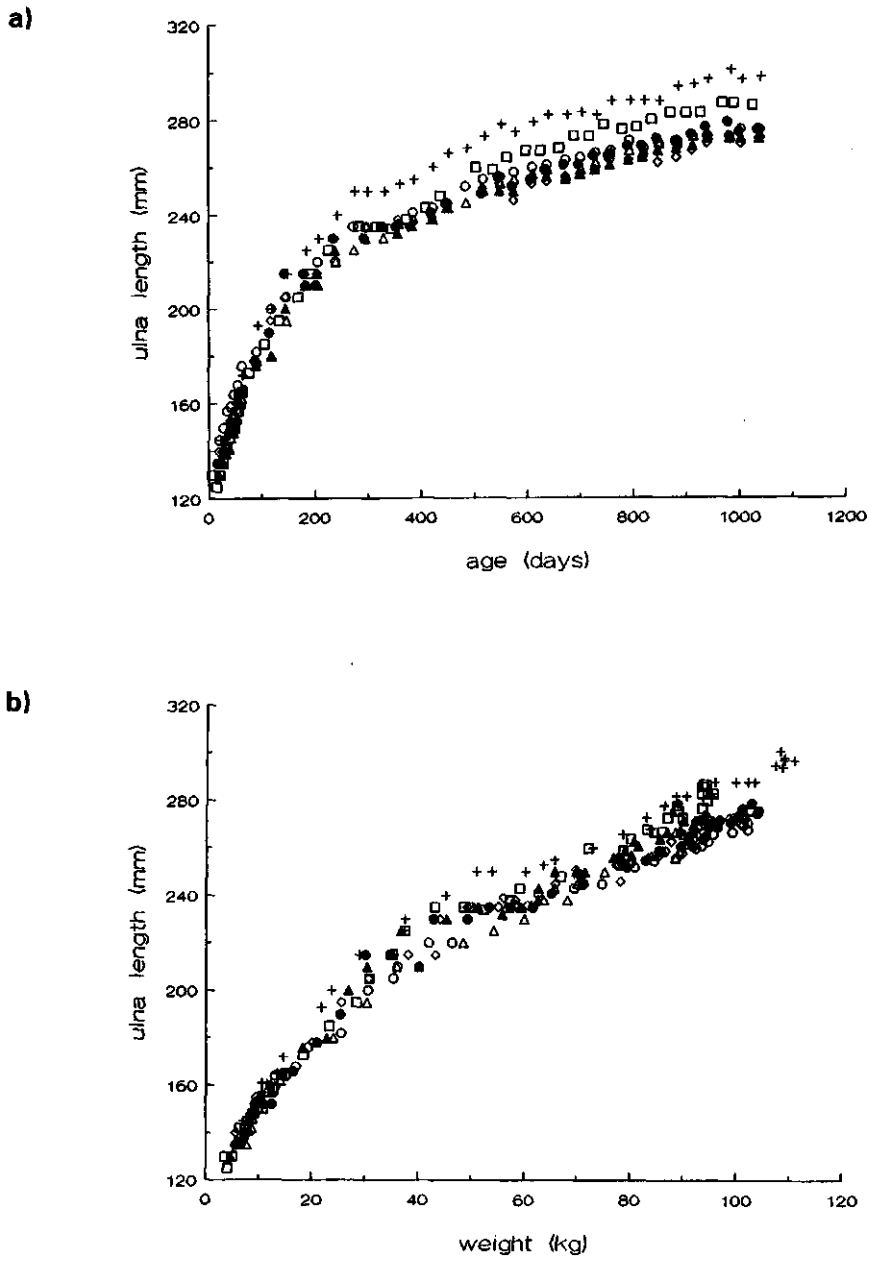


FIGURE 2. ***a)*** *Development of ulna length (mm) versus age (days) of 7 castrated Saanen goats,* ***b)*** *development of ulna length (mm) versus weight (kg) of the same goats; observations marked with different symbols for each goat.*

larger. It is not clear whether a larger frame size also could have an impact on the maximum weight that can be attained. If so, this complicates comparisons between intact and castrated animals of genetic size based on maximum weight. The conclusion to be drawn in this section is that in particular mature bone length offers perspectives as a practical measure of genetic size. This measure, however, is less well suited when early castrated animals are studied.

Measures based on allometric growth characteristics

In this section two methodological approaches will be discussed which provide information on genetic size from allometric growth patterns. The first one is based on the phenomenon of allometric 'transposition' as observed first by Meunier (1959), and enables quantification of genetic size differences from transpositions or shifts in allometric growth patterns. These transpositions in growth allometry are the inevitable result of scaling up or down of body size. Allometric transpositions were also observed in the experiment. Their value as genetic size indicators will be discussed with respect to body dimensions. The second methodological approach utilizes transition zones in multiphasic allometry as a reference basis for developmental stage and genetic size.

Allometric transposition as a result of size-scaling

As indicated earlier in Chapter 1, two basically different types of allometry are to be distinguished: ontogenetic or growth allometry versus static allometry. Body components may have different allometric coefficients for both types. This is illustrated by the growth coefficient for Ulna length relative to weight. In the experiment Ulna length had a value of 0.26 for both the Saanen goats and WAD goats of group DH (Chapter 5). The static coefficient of the ulna, which represents the allometric relation between genotypes at equivalent developmental stages, has an expected value of 1/3 if we assume that body shape remains the same at equal developmental stage. If the static coefficient and the growth coefficient of a body component appear to be different, ontogenetic allometric relationships of different sized genotypes that are equally sloped show the phenomenon of *allometric transposition*. This size-induced transposition is reflected by different intercepts of the allometric regression lines.

The transposition phenomenon was first observed by Meunier (1959) in species of gulls. The relationships between size and transposition and their effect on parameter a of the (ontogenetic) simple allometric relationship was further elaborated by White and Gould (1965). This relationship can be best understood if we study the effect of an increase in genetic size on logarithmic scale. In Figure 3a the allometric development of a one-dimensional body measure against weight is illustrated for two genotypes of which the larger one is a size-scaled version of the smaller and retains the same body shape. In this example the ontogenetic allometric coefficient is assumed to be smaller than 1/3. The increase in genetic size is reflected by a constant shift along the X-axis, since any proportional increase is converted into an additional increase on log-scale. If shape is to be maintained in the larger animal at equal developmental stage (i.e. at equal proportions of the adult weight), the figure shows that the ontogenetic allometric line *must* shift toward a higher level and the ontogenetic allometric slope in the larger animal *must* remain unchanged.

In fact, the increase in genetic size only affects the intercepts of the allometric lines. Gould (1971) expressed this effect of size increase from animal 1 to animal 2 in the following form, for cases where the static allometric coefficient had the value 1:

$$s = (a_1/a_2)^{1/(1-b)} \qquad (1)$$

where s represents the proportional size of animal 1 relative to animal 2, a_1 en a_2 are the parameters a from the simple allometric model in its arithmic form for both animals, and b is the common ontogenetic allometric coefficient. Gould (1971) called s the 'similarity criterion'. From Figure 3a it may be seen that the implications of size increase can also be formulated in a more general logarithmic form:

$$s_d = a_d/(b_s - b_o) \qquad (2)$$

where s_d stands for the log-difference in genetic size, thus representing the shift along the X-axis, a_d is the difference between log(a) of both animals, representing the shift along the Y-axis, b_s the static allometric coefficient, and

b_o the ontogenetic allometric coefficient. If b_s and b_o are known, s_d can be estimated from the allometric transposition.

It should be noted that these equations express the most direct form of genetic size scaling. In biological reality, the values of b_o may have changed among different sized genotypes of the same species indicating other modifications than scaling of size alone. It should also be noted that b_s may not always be known. Both in mammals and birds, these b values relative to body weight are not simply 1 for many components. For example in a number of body organs, values are reported that are lower than 1 (Peters, 1983).

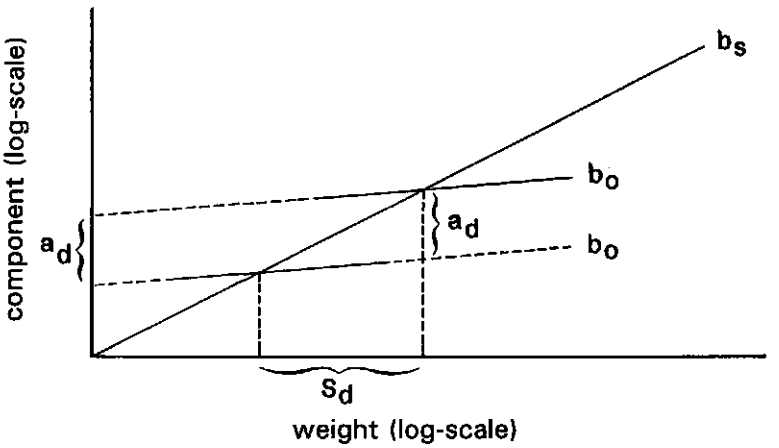
Allometric transposition in the experiment

Results from the cross-sectional and longitudinal analyses indicated that ontogenetic allometric coefficients were in general very consistent between both breeds. In view of the earlier outlined effects of genetic size changes on ontogenetic allometry, this consistency can be interpreted as an indication that the observed breed effects are mainly the result of a difference in genetic size. Yet it should be realized that, despite equal b_o values among breeds, still other than pure size-scaling effects may have been part of the breed effect, as will be demonstrated hereafter.

The following discussion will be restricted to quantification of scaling effects in the experimental breeds on basis of body dimension development relative to weight. It is assumed that body shape is independent of genetic size, i.e. b_s is expected to be 1/3 (length versus volume/weight). Prothero (1992) concluded from a study on body dimensions of adult terrestrial mammals that, in general, adult land mammals are geometrically similar along their major axes, which supports the assumed 1/3 value. Other components studied in the experiment might also have been considered, but here assumptions for static allometric coefficients would have been less firmly based. For reasons of simplicity, only the simple allometric relations will be considered, although it is noted that the same principles also apply to multiphasic patterns.

The longitudinal analysis showed that none of the body dimensions showed simple allometry for the whole observed weight range (Chapter 5). But analysis

a)



$$s_d = a_d/(b_s-b_o)$$

b_s = static allometric coefficient
b_o = ontogenetic allometric coefficient
s_d = difference in genetic size
a_d = allometric transposition

b)

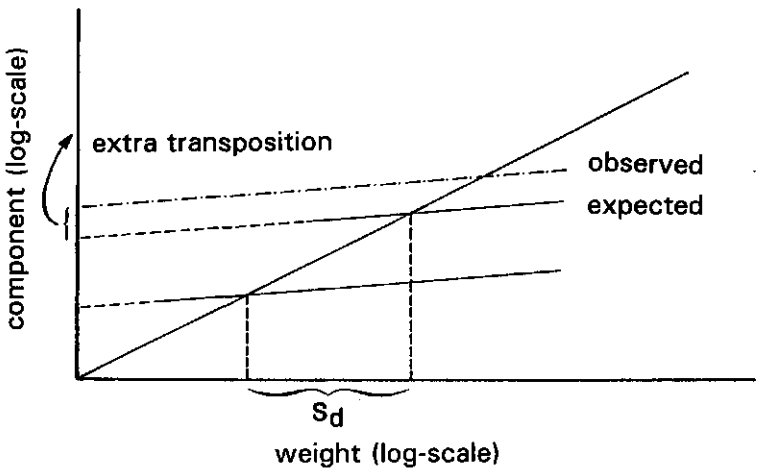


FIGURE 3. ***a)*** *Schematic representation of allometric transposition between two genotypes with different genetic size (see text),* ***b)*** *representation of extra allometric transposition as a result of size-independent genotypical differences.*

also indicated that trunk length (TL) and ulna length (UL) could be fairly well described in terms of simple allometry by splitting the data set into a preweaning and a postweaning part. Since the postweaning part represented the major part of the observational range, postweaning allometry in both breeds will be considered here only. Allometric characteristics of the Saanen breed will be compared with characteristics of WAD goats that were fed the same feed (group DH).

Table 3 of Chapter 5 shows that (ontogenetic) allometric coefficients for postweaning development of TL and UL were nearly the same, and indicates a significant deviation of these ontogenetic coefficients from the static coefficient 1/3. In order to apply equation (2), a common b value has to be used. In both dimensions the common b value is calculated as the mean of both breed values, for TL this is 0.283 and for UL 0.258. Before using these values in equation (2), the values of the parameters a have to be slightly adjusted on basis of the common b of each dimension, because these common b values differ somewhat from the specific breed values. Since the regression lines should pass the point that represents the mean log(LW) and the mean of log(UL) or log(TL), parameter a can be modified for each dimension by calculating in each breed the intercept of the line with the common b slope that passes through the forementioned point of means. Modifications in parameter a were very minor; modified a's of TL for the Saanen and the WAD breed were 5.521 and 5.389 respectively, those of UL were 4.429 and 4.280.

Applying the modified parameters to the equation resulted in the following log-estimates for a_d and s_d: respectively 0.132 and 2.623 for TL, and 0.149 and 1.991 for UL. The s_d values of TL and UL suggest considerably larger genetic size ratios than on basis of FFWA. The genetic size difference that is expressed by FFWA amounts 0.742 log units, or in other words the Saanen breed is 2.10 times larger than the WAD breed. In case of TL this ratio is 13.8 and in case of UL 7.3. These values have to be considered unrealistic high if compared to the other estimates available, that lie around 2.00-2.50. The reason for these unexpectedly high ratios have to be sought in an extra breed effect on UL and TL next to the pure size-scaling effects.

It can be calculated from equation (2) for both dimensions, how large the allometric transposition a_d would have been in case s_d would have been 0.742 as indicated by the breed difference in FFWA. The expected a_d values are 0.037 for TL and 0.056 for UL, substracting these values from the observed a_d values indicates that the observed *extra* transposition was 0.095 log units for TL and 0.093 log units for UL. In Figure 3b a schematic representation is given of this extra transposition. This extra transposition means that if we compare UL and TL of both breeds at equal proportions of their FFWA, the Saanen is consistently 10.0% longer in TL and 9.7% longer in UL. These proportional deviations are of the same order and suggest that if we would have calculated the s_d on basis of the ratio TL/UL, instead of the single components, the estimated size difference would have been much more in line with other estimates. Indeed, the calculated s_d on basis of the ratio TL/UL indicates a breed ratio of 2.00, and agrees much better with other estimates.

Apparently, body shape is not completely similar for both breeds. The example illustrates how combined size-scale effects and size-independent effects may lead to equal ontogenetic allometric coefficients. Interpreting allometric transposition simply in terms of pure size scaling effects therefore can be very misleading. On the other hand, once size differences are known, analysis of allometric transposition effects can be very useful to identify typical size-independent genotypical effects. The example also underlines that whatever measure is taken as an indicator of genetic size, care should be taken that the genetic variation expressed by this measure is as closely as possible related to genetic size variation. Bone length measures may possibly contain more extra size-independent genetic variation than measures based on body mass. This aspect should be included in studies which investigate the suitability of bone lengths as measures of genetic size. Defining measures on basis of ratios of bone lengths or combinations of bone lengths could be a better alternative if it can be shown that they are less subject to extra genetic variation. The use of combinations of body measurements was recommended earlier by Tanner (1977). He proposed to use a combination of body measurements for quantifying body shape which excluded effects of final size, in order to have and adequate measure for developmental maturity of humans.

It is concluded here that allometric transposition represents a phenomenon that deserves more attention in allometric studies than so far given in literature. Allometric transposition can be of particular interest for quantifying differences in genetic size. Understanding of allometric transposition leads to a better interpretation of parameter a, which is very often ignored in allometric studies. Understanding of transposition also shows that ontogenetic allometric coefficients can be expected to be similar between differently scaled bodies, although other size-independent genotypical effects may also be involved as shown by the example.

Genetic size measures based on multiphasic allometric growth

The results from Chapter 3, 4 and 5 made clear that multiphasic analysis of allometric growth gave a markedly better description and more insight for a number of body components than could have been provided by the simple single-phased approach. The observed consistency among breeds and feed quality groups supported the multiphasic approach. Describing their growth relative to the fatfree component instead of the whole EBW proved to be of vital importance in unveiling the phasic nature of development patterns in the cross-sectional slaughter data. Otherwise, inclusion of the fat component would have complicated interpretation of the results, since it would not have been clear whether phasic patterns were due to the described component or to phasic effects of the fat component. In principle, it can be argued that the same problem applies to phasic components of the fatfree weight studied in the experiment. Yet, their effect can never be that dominant as for fat because they are proportionally much smaller than the fat component.

As indicated earlier, multiphasic analysis is of special interest to size determination because of identification of transitional zones. In Figure 4 an overview is given of the location of these zones relative to the development of fatfree weight for both experimental breeds; besides cross-sectional data, chest girth and birth weight are also included. On this fatfree scale, it can be seen that all transitions occurred before 50% of FFWA has been reached, underlining the importance of these early developmental stages for organ growth. For most components, breed differences were relatively small, ranging from 0 to 20% of FFWA, except for the liver, which was considerably larger. The transition zones

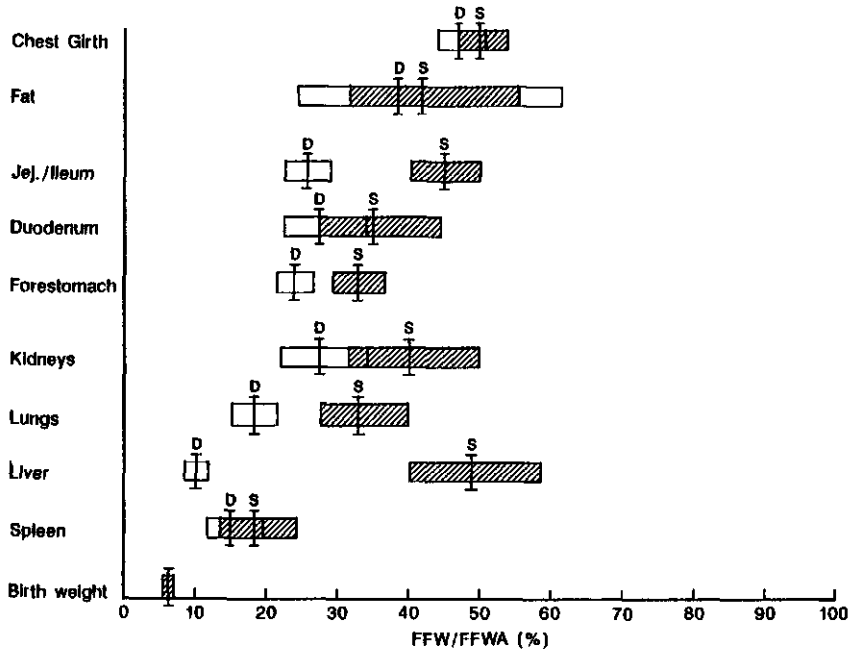


FIGURE 4. *Transition zones (± standard errors) of diphasic organs, transition of chest girth, and birth weight as percentages of the fatfree component of asymptotic weight (FFW/FFWA), for the Saanen breed (S) and the WAD-goats (D) of group DH.*

of the WAD breed were consistently at a lower rate of maturity than those of the Saanen breed. This means that breed ratios of genetic size, calculated on basis of fatfree weights at these transitional zones, are all larger than the FFWA ratio. These different breed ratios illustrate that other effects than pure size scaling contributed to the observed breed differences.

From a practical point of view, it is evident that measures based on external observations are to be preferred over measures that rely on cross-sectional slaughter data. Cross-sectional data are not suited for individual estimates of genetic size, they are more difficult to obtain, and animals have to be sacrificed. Among the observed multiphasic body characteristics, only chest girth could be externally measured. As outlined before in Chapter 5 and as can be seen from Figure 4, transition of chest girth is closely located near the transitional levels of fat for both breeds, and it was suggested earlier that the increase in chest

growth relative to LW was linked to the acceleration in fat development and not to bone. This suggested link demonstrates how analysis of cross-sectional slaughter data can be utilized to yield a better understanding of external multiphasic patterns.

Chest girth, however, is of limited value as a practical measure for genetic size when used for individual estimates. Individual asymptotic standard errors of weight at transition, generally, proved to be large (not reported in this thesis). Probably they would have been smaller when measures were more frequently taken than monthly. Inevitably, however, chest girth will always include larger measurement errors than bone measures, since the latter are much less dependent on the animal's standing position. When used for size determination of groups of animals, these problems can be overcome by including sufficient numbers of animals in the analysis. Indeed, Figure 4 shows that the standard errors related to chest girth transition behaved favourably compared to those of the organs. For calculation of breed ratios they are even more favourable because here the proportional size of the standard error is important instead of the absolute errors that are indicated in the figure.

Another practical problem is that an accurate determination requires observations in a sufficiently extended weight range after transition. Since this transition occurs after the transition in fat development, animals have to enter a considerable part of the second fattening stage to enable observations at sufficiently high weight levels. Breeding animals may not reach such high weight levels in practice. Yet, if we demand that the length of the observed weight range in the second phase should be at least half of the range of the first phase, it can be demonstrated that animals do not have to grow beyond normal weight ranges of breeding animals. For example, LW at transition in WAD goats was estimated at 17 kg (taking the mean of DH and DL; Chapter 5, Table 2) and chest girth therefore should be recorded up to a weight of 25.5 kg, which is lying in the weight range of 20 to 30 kg for breeding animals of the experimental WAD flock.

It is concluded that, despite the mentioned practical limitations, the experimental data demonstrated that it is possible to determine breed ratios of

genetic size from external measures that have multiphasic development patterns. If sufficient animals are included, a high accuracy can be reached for group means. The measure refers to a normal developmental level that is reached by all breeding animals, contrary to asymptotic measures. No animals have to be sacrificed for this determination, contrary to measures based on cross-sectional data. If multiphasic patterns could be used of bone dimensions, which can be more precisely measured, this approach offers perspectives for individual determination of genetic size at an earlier stage of development than full maturity.

OVERALL CONCLUSIONS AND PROSPECTS

In this final chapter a number of measures have been discussed in view of selecting a more practical and accurate measure of genetic size than adult weight. The major conclusion to be drawn from this discussion is that, although limited in number, some measures offer perspectives for improvements that enable a better use of the genetic size-scaling theory. Their applicability depends mainly on the purposes for using genetic size measures. If used as a trait in breeding programmes based on progeny testing on farm, possibilities are far more limited than in case of breeding on station. If used in experiments, measures may be used that require extended longitudinal recordings of growth characteristics or slaughtering data.

On farm level, the only practical measures for breeding purposes are offered by adult bone length dimensions. These stable measures can be relatively simply recorded in farm animals at any time after sexual maturation when bone length growth has ceased. Without doubt, part of the variation in bone length is independent of genetic size, as shown in the experiment for ulna length. To minimize this type of variation, combined sets of measures should be used that reflect the total body frame, instead of single measures.

In many production systems breeding programmes can only be implemented on station level. On this level, there is a wider scope for application of genetic size measures in genotype evaluation, since information can be collected more

frequently in a controlled environment. Simple longitudinal measurements of bone lengths, other body dimensions and weight development enable estimates of genetic size measures based on asymptotic bone lengths and transition weights in multiphasic allometric patterns. This study demonstrated how multiphasic allometry observed in chest girth can be utilized for this purpose. Especially in crossbreeding programmes with differently sized breeds, this type of information is essential to distinguish between pure size-scale effects and other size-independent effects.

On experimental level, measures of genetic size may rely on more information and may be more elaborate than would be acceptable for breeding programmes. However, they should be obtained from growth characteristics during the normal stage of growth and not from maximum weight levels that are far beyond normal equilibrium weights. It has been shown in this chapter, how use can be made of allometric growth patterns. Despite the useful properties of allometric characteristics of body components for size determination, a major set-back remains that many of them rely on cross-sectional slaughter data. There is a strong need for better, more reliable, inexpensive methods for *in vivo* determination of body composition. More recent techniques like NMR and CT-scanning should be used on a much wider scale in animal production research. Longitudinal observations in development of body composition will reveal much more detail and understanding than can ever be reached in cross-sectional designs, especially in animal groups that contain much individual genetic variation.

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GENERAL CONCLUSIONS

1. Genetic size measures are available that offer perspectives for a more accurate and practical determination of genetic size than a measure based on adult weight.

Results from the experiment demonstrated that genetic size measures could be derived from a number of different growth characteristics. Measures based on body dimensions, in particular bone lengths, are of interest, as they have a stable character and are relatively easy to measure. This study showed how chest girth development can be utilized for genetic size determination.

2. Allometric growth patterns are very useful in early determination of genetic size. Allometric transposition, and transition in multiphasic allometry yield information on genetic size.

Understanding of allometric transposition contributes to a meaningful interpretation of the intercept parameter in both the simple allometric model and multiphasic allometric model. Transition zones in multiphasic patterns represent specific growth stages that may serve as reference basis for size determination.

3. Analysis of (multiphasic) allometry in body components should be based on fatfree weight as the explanatory variable.

Inclusion of the fat component in the explanatory variable complicates interpretation of results, since fat exhibits a multiphasic development patterns relative to fatfree weight.

4. Size determination on basis of body dimensions is more complicated in castrated animals than intact animals.

Epiphyseal closure in intact animals, will result in multiphasic allometric patterns for long bone lengths. In this experiment, castrated animals showed no epiphyseal closure. Growth experiments in which genetic size is quantified on basis of body dimensions therefore should include intact animals.

5. Equal degree of maturity in terms of proportions of genetic size is a more stable basis for comparison of genotypes than metabolic age.

The two WAD groups that were fed different feed qualities showed similar development patterns at equal proportions of their asymptotic weight, whereas on equal metabolic age basis groups differed in development. When compared at equal metabolic age the Saanen breed was more developed than the WAD breed, whereas at equal proportions of asymptotic weight they were at more similar levels of development.

6. At equivalent developmental stages, allometric growth patterns were very similar for the Saanen breed and the WAD breed, the size-scaled feed intake of the Saanen goats was higher than intake of the WAD goats, and the efficiency in the conversion of feed into gain was higher in the observed developmental range.

Consequently, Saanen goats were developing faster than expected on basis of the size difference with WAD goats. At equal age, Saanen goats appeared to be at the same degree of maturity as WAD goats. This should not be interpreted, however, as a general intra-specific scaling effect, but as an example of how breeds may differ from the standardized mammalian growth curve. The observed consistency in allometric growth patterns among both breeds underlines the similarity of their growth programmes if compared at a size-independent basis.

7. Use of the genetic size-scaling theory provides a powerful method for elimination of animal variation due to different stages of development and genetic size, and contributes to a better understanding of genotypical differences.

Proper analysis of growth data depends on the ability to correct for sources of variation other than those under study. The genetic size-scaling theory enables a desegregration of genetic size effects and size-independent effects. Analysis of growth of the two goat breeds under study made clear that use of the genetic size concept was indispensable for understanding of breed differences.

SUMMARY

Since the last century, many biologists have studied the effects of size differences between species on the rate of their metabolic processes. In 1980, Taylor published the genetic size-scaling theory which incorporated the existing knowledge on size effects, and introduced two formal scaling rules and the concept of genetic size. Genetic size is expressed at all developmental stages of growth, but is most clearly visualized by the size of the mature animal; usually genetic size is quantified by the weight of the mature animal. In the scaling theory, genetic size is defined as the major genetic factor that controls the growth rate of an organism from its early embryonic stages to full maturity, and continues to determine rate and duration of life processes during the remaining part of life.

The genetic size-scaling theory states that variation between animals can partly be explained by differences in scale, expressed by the genetic size factor. By applying scaling rules, the differences in scale can be eliminated. What remain are size-independent differences. The size scaling theory may be very useful for animal breeding, as it provides a biological basis for explaining genetic variation. In practice, breeding is mainly based on selecting fast growing animals for meat production and high yielding animals for milk and egg production. These traits include variation due to differences in genetic size. Genetic size, however, is not related to the individual biological efficiency. If it would be possible to define size-independent traits, selection on biological efficiency would be more effective. Especially in tropical animal production systems, application of the genetic size concept can be very fruitful for a proper breed evaluation of differently sized indigenous breeds, imported exotic breeds and their crossbreeds.

As outlined in the general introduction of this thesis, concepts of genetic size are not adopted in animal production mainly due to the lack of a more precise and practical measure than adult equilibrium weight. This study was undertaken to solve some of the implementation problems. The objectives of this thesis were:

1. To improve the practical applicability of the genetic size scaling theory at the individual genotype level and at the breed level. The study particularly focused

on exploration of alternative measures for genetic size.
2. To elaborate methods for evaluation of growth characteristics among individual genotypes and breeds which incorporate the genetic size concept, and which enable assessment of the relative importance of genetic size in breed differences.

Chapter 1 of this thesis starts with a brief overview of the main developments in the study of metabolism and scaling, from the initial surface law, the mouse-to-elephant curve, to the genetic size-scaling theory. The outline served to identify areas where additional basic research is needed for successful application of the genetic size-scaling theory in practice. Two basic problems were identified: rules for intra-specific scaling are not firmly established, and a practical accurate method for size determination is lacking. Conditions for an ideal practical measure of genetic size were formulated, and current methods for size determination in ruminant species were discussed. It was concluded that a promising approach for determination of genetic size is to look for characteristics in (relative) growth patterns of body components that are linked to functional stages of development.

In order to gain more insight into the effects of genetic size and possible measures, a long term experiment with two goat breeds was carried out. Data on growth, *ad libitum* feed intake, body composition and body frame development of castrated males were recorded during 3 years (1987-1990) from birth to a weight level near the asymptotic weight. The two goat breeds used in the trial differed widely in adult size: the Saanen breed, a large sized European dairy breed, and the West African Dwarf goats (WAD goats), one of the smaller goat breeds. After weaning, the Saanen breed (group S) and half of the WAD animals (group DH) were fed pellets of feed H (10.7 MJ ME/kg DM). The other half of the WAD animals (group DL) received pellets of feed L (7.5 MJ ME/kg DM). A serial slaughtering scheme was designed to examine the changes in body composition. Breed effects were analyzed by comparing group S with DH, and feed effects by comparing group DH with DL.

In Chapter 2, animal management, feed composition, digestibility experiments and other experimental methods related to the recording of feed intake and growth were described in detail. An integrated feed intake and growth model

was presented, based on the relationships between respectively weight (W) and cumulative feed intake (F), and W and age (t). The models were fitted to longitudinal data sets of 10 animals of group S, 8 of DH and 8 of DL and breed and feed quality effects on animal variation were examined for each model parameter. Feed quality did not affect the asymptotic weight (A) of the WAD goats (DH, 48.1 kg; DL, 52.1 kg). The feed intake curve against u (=W/A) of DH, was more convex in approaching adult intake than the curve of DL. The feed efficiency parameter (AB) was lower for the L feed (DH, 0.262; DL, 0.172). The maturation rate (du/dt) of DL was lower than the rate of DH. There was a strong breed effect on A (S, 109.6 kg versus DH, 48.1 kg). The shape of the size-scaled feed intake curve was similar for S and DH, but its magnitude was at comparable u higher for S. At u = 1 the estimated scaled intake of S was 1.18 times the intake of DH. Group S converted their feed more efficiently than DH (AB for S: 0.291). There was no breed effect on du/dt. Size-scaling of the time component dt by $A^{0.27}$ in maturation rate du/dt, resulted in a higher scaled maturation rate for S. It was concluded that in this specific case, growth traits of both breeds could be better compared on basis of normal age than scaled age.

In Chapter 3, breed and feed quality effects on body composition were studied. Cross-sectional slaughter data, that covered postnatal growth over a period of nearly 3 years, of 27 animals of group S, 31 of DH, and 31 of DL were used in the analysis. Water, protein and ash accretion were described against fatfree weight (FFW) by the simple allometric model. The allometric coefficients (b) showed a very consistent pattern among the groups, with minor effects of breed and feed. For all groups, FFW showed a decreasing water proportion toward maturity accompanied by higher protein and ash proportions. Fat deposition was described against FFW by a diphasic allometric model. The extra phase improved the fit for S and the combined DH and DL group. Feed quality did not affect b in both phases, nor the FFW level at which the second phase started. S had a higher b than DH in the first phase, and the same in the second. S entered the second phase at a higher weight than DH, but this could be mainly attributed to their larger genetic size. It was concluded that the consistency in parameters of the diphasic allometric model among breed and nutrition groups supported the concept of distinct phases of fat growth.

In Chapter 4, effects on growth of lungs, heart, liver, kidneys, spleen, forestomachs, abomasum, duodenum, jejunum/ileum and the humerus bone were examined by both monophasic and multiphasic analysis of their growth relative to FFW. Cross-sectional data of the animals of Chapter 3 were used. Analyzed organs were consistently single-phased or diphasic in both breeds. The same consistency, except for heart, was observed among both feed quality groups. Only heart growth (for S and DH only), and abomasum and humerus were single-phased. The allometric coefficients of the diphasic organs indicated in their first phase a proportional increase of organ and thereafter a proportional decrease. The goats in DL developed a larger digestive tract, heart, kidneys and liver than goats of equal weight in DH. The breeds had very similar allometric coefficients, which differed only for the second phase of the lungs and jej./ileum, and for both phases of the liver. The main part of the breed variation was expressed by genetic size-dependent parameters. The consistently higher weight levels at transition for group S reflected the larger genetic size of the Saanen breed.

In Chapter 5, breed and feed quality effects on chest girth (CG), length of trunk (TL) and ulna (UL) were examined by monophasic and multiphasic analysis of their growth relative to W. Longitudinal data of 15 animals of group S, 12 of DH and 9 of DL were used. Allometric coefficients from the monophasic allometric model indicated proportional enlarging of CG, and decreasing of TL and UL. The diphasic model described CG better than a monophasic model. Allometric coefficients increased from the first (0.31) to the second phase (0.45), and were not affected by breed or feed. Breed estimates of transition zones between phases in CG could serve as indicators of genetic size. TL and UL were not fitted adequately by a diphasic model. However, separate analyses of preweaning and postweaning growth improved the overall monophasic fits in most cases. Monophasic residuals of UL showed systematic changes in postweaning growth patterns, and indicated the absence of epiphyseal closure in these castrated animals.

In Chapter 6, the results and conclusions of the foregoing chapters were integrated to evaluate genetic size measures that are accurate and practical in use. Different types of genetic size measures were assessed on basis of criteria outlined in Chapter 1. It was concluded that asymptotic weight (A) is not a

suitable measure to describe genetic size of animals in normal animal production environments. Among body component-age relations, in particular bone lengths offer perspectives; mature bone lengths or characteristics from multiphasic analysis could be applied. However, size determination on basis of bone length can be complicated in castrated animals. Both simple allometry and multiphasic allometry provide information on genetic size. It is explained how the phenomenon of allometric transposition is related to genetic size differences. Transition zones in multiphasic allometry can be used as genetic size indicators. Multiphasic allometry in chest girth offers a possibility to determine genetic size from an external measure. It was concluded that, although limited in number, some measures offer perspectives for improvements that enable a better use of the genetic size-scaling theory. Prospects for use of genetic size measures at production level and experimental level were briefly discussed.

The following general conclusions were drawn:

1. Genetic size measures are available that offer perspectives for a more accurate and practical determination of genetic size than a measure based on adult weight.
2. Allometric growth patterns are very useful in early determination of genetic size. Allometric transposition, and transition in multiphasic allometry yield information on genetic size.
3. Analysis of (multiphasic) allometry in body components should be based on fatfree weight as the explanatory variable.
4. Size determination on basis of body dimensions is more complicated in castrated animals than intact animals.
5. Equal degree of maturity in terms of proportions of genetic size is a more stable basis for comparison of genotypes than metabolic age.
6. At equivalent developmental stages, allometric growth patterns were very similar for the Saanen breed and the WAD breed, the size-scaled feed intake of the Saanen goats was higher than intake of the WAD goats, and the efficiency in the conversion of feed into gain was higher in the observed developmental range.
7. Use of the genetic size-scaling theory provides a powerful method for elimination of animal variation due to different stages of development and genetic size, and contributes to a better understanding of genotypical differences.

SAMENVATTING

Sedert de vorige eeuw hebben veel biologen onderzocht hoe de variatie in volwassen grootte tussen diersoorten samenhangt met de snelheid waarmee hun metabolische processen verlopen. De bestaande kennis op dit gebied werd door de Britse onderzoeker Taylor aangewend voor het opstellen van de "genetic size-scaling theory", hetgeen woordelijk de "genetische grootte-schalingstheorie" betekent en hier verder wordt aangeduid als de schalingstheorie. In deze in 1980 gepubliceerde theorie werd het begrip "genetische grootte" geïntroduceerd en twee schalingsregels. Genetische grootte is een genetische factor die tot uitdrukking komt gedurende het gehele proces van ontwikkeling, maar het meest duidelijk tot uiting komt als de grootte van het volwassen dier. Gewoonlijk wordt het volwassen gewicht als maat voor genetische grootte genomen. In de schalingstheorie werd genetische grootte gedefinieerd als de genetische factor welke de groeisnelheid van een organisme bepaalt waarmee het zich ontwikkelt van embryo tot het volwassen stadium, en tevens de snelheid van de metabolische processen medebepaalt voor de rest van het leven.

Volgens de schalingstheorie kan diervariatie gedeeltelijk verklaard worden door verschillen in een schaal, die wordt bepaald door de genetische grootte. Door het toepassen van schalingsregels kunnen deze verschillen geëlimineerd worden, en kunnen de grootte-onafhankelijke verschillen zichtbaar gemaakt worden. De schalingstheorie geeft een biologische verklaring voor genetische variatie en is hiermee van belang voor dierlijke produktie. De huidige fokkerij richt zich hoofdzakelijk op selectie van snelgroeiende dieren voor vleesproduktie en dieren met hoge produkties voor b.v. melk of eieren. De hierbij gebruikte kenmerken zijn deels afhankelijk van genetische grootte. Door de genetische grootte-component in deze kenmerken te elimineren zou selectie op een effectievere wijze kunnen leiden tot efficiëntere dieren, aangezien deze grootte-component niet samenhangt met individuele biologische efficiëntie. Met name in tropische veehouderijsystemen kan toepassing van de schalingstheorie van belang zijn voor een juiste waardering van de, qua grootte zeer uiteenlopende, inheemse en geïmporteerde rassen en hun talrijke kruisingen.

Tot dusver wordt het genetische grootte concept niet gebruikt in de praktijk vanwege twijfels over een geschikte maat voor genetische grootte. Dit

proefschrift, getiteld: "Genetische grootte en groei van geiten", beschrijft onderzoek naar een geschikte maat welke nauwkeuriger en praktischer is dan volwassen gewicht. In de Algemene Introductie werden de volgende doelstellingen geformuleerd:

1. Verbetering van de praktische toepasbaarheid van de schalingstheorie op zowel individueel dierniveau als rasniveau. De studie spitste zich toe op het zoeken naar alternatieve maten voor genetische grootte.

2. Aandragen van methoden voor het vergelijken van groeikenmerken tussen individuele dieren en tussen rassen, gebaseerd op het concept van genetische grootte, waarbij het belang van variatie als gevolg van grootte-verschillen duidelijk wordt.

Het proefschrift begint in hoofdstuk 1 met een kort historisch overzicht van het onderzoek naar de relaties tussen lichaamsgrootte en de snelheid van metabolische processen. Hierin komen onder meer de oppervlakte-wet van Sarrus en Rameaux, de muis-tot-olifant curve van Brody, en Taylor's schalingstheorie aan de orde. Het doel van dit overzicht was aan te geven waar aanvullend onderzoek gewenst is voor succesvolle praktische toepassing van de schalingstheorie. Twee kernproblemen werden gesignaleerd: het is niet voldoende zeker of schalingsregels tussen soorten ook binnen soorten mogen worden toegepast, en er ontbreekt een exacte en praktische maat voor genetische grootte. De voorwaarden waaraan een geschikte maat moet voldoen werden geformuleerd, waarna de huidige methoden voor grootte-bepaling werden besproken. Geconcludeerd werd dat mogelijk bruikbare maten kunnen worden gebaseerd op karakteristieke stadia in relatieve groeipatronen van lichaamscomponenten.

Teneinde een beter inzicht te verkrijgen in de effecten van genetische grootte en mogelijke maten hiervoor, werd een langlopend groei-experiment met twee geiterassen uitgevoerd. Gegevens werden verzameld van mannelijke gecastreerde dieren welke betrekking hadden op groei, *ad libitum* voeropname, lichaamssamenstelling en ontwikkeling van lineaire lichaamsmaten, vanaf geboorte tot dichtbij het maximaal haalbare gewichtsniveau over een periode van 3 jaar (1987-1990). De geiten in de proef waren van het Saanen ras, een

relatief groot Europees melkras, en van het West-Afrikaanse Dwergras (WAD-ras), een klein tropisch vleesras. De Saanen geiten (groep S) en de helft van de WAD-geiten (groep DH) ontvingen na spenen het gepelleteerde voeder H (10.7 MJ ME/kg DS). De andere helft van de WAD-geiten (groep DL) ontvingen pellets met een lagere energieconcentratie, voeder L (7.5 MJ ME/kg DS). Raseffecten werden geanalyseerd door groep S met groep DH te vergelijken, en voedereffecten door groep DH met DL te vergelijken.

In hoofstuk 2 werden de algemene aspecten van de proef op het gebied van management, gebruikte voeders en bijbehorende verteringsproeven in detail beschreven. In dit hoofdstuk werden de effecten van ras en voerkwaliteit op voeropname en groei onderzocht. De analyse werd uitgevoerd m.b.v. een geïntegreerd voeropname- en groeimodel, gebaseerd op de relaties tussen lichaamsgewicht (LW) en cumulatieve voeropname, en LW en leeftijd (t). Er werd gebruik gemaakt van longitudinale gegevensbestanden, d.w.z. bestanden met herhaalde waarnemingen van één dier. De waarnemingsreeksen werden per dier geanalyseerd en in parameters uitgedrukt, waarna de effecten van ras en voerkwaliteit op de diervariatie in elke parameter werden onderzocht. Alle vergelijkingen werden uitgevoerd op basis van een gelijk groeistadium (u), welke werd uitgedrukt als fractie van het asymptotische gewicht (A). Voerkwaliteit had geen statistisch significante invloed op parameter A van groep DH (48.1 kg) en DL (52.1 kg). De voeropnamecurve t.o.v groeistadium u liet in groep DH een meer convex verloop naar de maximale opname zien dan in DL. De efficiëntie waarmee de verteerbare voerenergie werd benut lag aanzienlijk hoger voor voeder H. De gemiddelde waarde voor parameter A van de Saanen geiten was 109.6 kg. Op basis van de schalingstheorie mocht worden verwacht dat de genetisch grotere Saanen geiten op gelijke leeftijd in een fysiologisch jonger groeistadium verkeren dan de WAD geiten. Als gevolg van een hogere geschaalde opname en betere voerefficiëntie bij de Saanen geiten, bleek in dit specifieke geval echter dat deze op gelijke leeftijd even ver ontwikkeld waren als de WAD geiten.

In hoofdstuk 3 werden de ras- en voereffecten op de chemische lichaamssamenstelling onderzocht. Ter bestudering van de ontwikkeling van de lichaamssamenstelling werd een transversaal slachtschema gehanteerd, d.w.z. uit opeenvolgende leeftijdsintervallen werden telkens enkele dieren voor analyse

genomen. De aanzet van water, eiwit en as werd beschreven als functie van het vetvrije lichaamsgewicht (VVLW) met het simpele allometrische model: $\log(y) = a + b \log(x)$. In dit model geeft de allometrische coëfficiënt b een proportionele toename ($b > 1$) van y of afname ($b < 1$) t.o.v. x weer. De b-waarden lieten voor elke component een consistent beeld tussen de groepen zien, met slechts geringe ras- en voereffecten. De hoeveelheid water in het VVLW nam proportioneel af met het toenemen van het VVLW, en de hoeveelheid eiwit en as namen proportioneel toe. De vetaanzet werd beschreven met een tweefasig allometrisch model. Dit model gaf zowel voor groep S als voor de gecombineerde dataset van DH en DL een betere beschrijving dan het (enkelfasige) simpele allometrische model. Voerkwaliteit bleek geen invloed te hebben op de b-coëfficiënten van beide fasen van vet, noch op het VVLW-niveau tijdens de fasenovergang. De Saanen geiten hadden een iets hogere b-waarde dan de DH-geiten in de eerste fase, en een gelijke b-waarde in de tweede fase. De grotere genetische grootte van de Saanen geiten werd weerspiegeld door het veel hogere niveau van het VVLW op de fasenovergang. Geconcludeerd werd dat de sterk met elkaar overeenkomende b-waarden in beide fasen, ongeacht ras of voerkwaliteit, de veronderstelling ondersteunen dat vetaanzet gefaseerd plaatsvindt.

De ontwikkeling van longen, hart, lever, nieren, milt, voormagen, lebmaag, duodenum, dunne darm en de humerus werd in hoofdstuk 4 beschreven. De componenten werden met enkelfasige en tweefasige allometrische modellen beschreven, met het VVLW als verklarende variabele. De organen waren in beide rassen consistent enkelfasig of tweefasig. Hetzelfde gold voor de voederkwaliteitsgroepen, uitgezonderd het hart. Alleen lebmaag, humerus en hart (enkel in S en DH) waren enkelfasig in ontwikkeling. De b-waarden van alle overige tweefasige organen lieten een proportionele toename van orgaangrootte in de eerste fase zien ($b > 1$), gevolgd door een afname in de tweede fase ($b < 1$). Op een gelijk VVLW-niveau hadden de DL-geiten een zwaarder verteringsstelsel, hart, lever en nieren dan de DH-geiten. De groeipatronen kwamen voor beide rassen sterk overeen. De b-waarden verschilden alleen voor beide fasen van de lever, en voor de tweede fase van longen en dunne darm. Het grootste deel van de rasverschillen kwam tot uitdrukking in de hogere gewichtsniveaus van de Saanen geiten op de fasenovergang, wat inhoudt dat het rasverschil hoofdzakelijk werd veroorzaakt door het genetische grootte-verschil.

In hoofdstuk 5 werd de ontwikkeling van de lineaire lichaamsmaten geanalyseerd. De ontwikkeling van borstomvang (BO), romplengte (RL) en ellebooglengte (EL) t.o.v. LW werd met enkel- en tweefasige allometrische modellen bestudeerd. De analyse was gebaseerd op longitudinale gegevens. Het tweefasige model beschreef BO beter dan het enkelfasige. De b-waarden namen toe van de eerste fase (b = 0.31) naar de tweede fase (b = 0.45), en bleken niet afhankelijk van ras of voerkwaliteit. Het gewicht op de fasenovergang voor elk ras zou kunnen dienen als een maat voor genetische grootte. RL en EL konden niet met een tweefasig model beschreven worden. Een gescheiden analyse van de gegevens vóór en na spenen op basis van enkelfasige modellen, resulteerde in een betere beschrijving dan een eenfasig model voor het gehele trajekt. De enkelfasige residuen van de fits van EL lieten systematische veranderingen in de groei na spenen zien; het groeipatroon gaf aan dat de betreffende groeischijven in deze gecastreerde dieren niet tot sluiting waren gekomen.

In hoofdstuk 6 werden mogelijk geschikte maten voor genetische grootte geëvalueerd, waarbij gebruik werd gemaakt van de resultaten en conclusies van de voorafgaande hoofdstukken. Op basis van de in hoofdstuk 1 geformuleerde criteria werden verschillende groepen van genetische grootte-maten beoordeeld. Geconcludeerd werd dat het asymptotische gewicht geen praktische en nauwkeurige maat is voor landbouwhuisdieren onder normale produktie-omstandigheden. In de groep van maten die afgeleid kunnen worden van component-leeftijdsrelaties, bieden met name de botlengtes perspectief op een geschikte maat. In het bijzonder volwassen botlengtes en karakteristieke ontwikkelingsstadia in meerfasige allometrie zijn van belang. Voor gecastreerde dieren zijn met name botmaten echter minder geschikt. Zowel enkelfasige als meerfasige allometrie geven informatie over genetische grootte. Uiteengezet werd hoe het fenomeen van 'allometrische transpositie' tussen genotypen samenhangt met genetische grootte-verschillen. Fasenovergangen in meerfasige allometrie zijn eveneens nauw gerelateerd aan genetische grootte. Eerder werd aangetoond hoe hierdoor, m.b.v. een eenvoudige uitwendige lichaamsmaat, genetische grootte-verschillen kunnen worden gekwantificeerd. De samenvattende conclusie was dat er aantal maten beschikbaar zijn, hoewel beperkt in aantal, die uitzicht bieden op een beter gebruik van de schalingstheorie. Aan het eind van dit hoofdstuk werd in het kort ingegaan op de vooruitzichten van de schalingstheorie voor experimenteel en meer praktisch gebruik.

Dit proefschrift werd afgesloten met de volgende algemene conclusies:

1. Er zijn maten voor genetische grootte beschikbaar die uitzicht bieden op een beter gebruik van de schalingstheorie dan een maat gebaseerd op volwassen gewicht.

2. Allometrische groeipatronen zijn van belang voor een vroegtijdige bepaling van genetische grootte. Zowel fasenovergangen in meerfasige allometrie als allometrische transpositie geven informatie over genetische grootte.

3. Voor een zinvolle analyse van allometrische groei van lichaamscomponenten moet gebruik gemaakt worden van vetvrij gewicht als verklarende variabele.

4. Bij gecastreerde dieren is de bepaling van genetische grootte d.m.v. lichaamsmaten gecompliceerder dan bij niet-gecastreerde dieren.

5. Bij het vergelijken van genotypen op basis van gelijke mate van volwassenheid, kan deze gelijke mate van volwassenheid beter worden uitgedrukt als proportie van genetische grootte dan als metabolische leeftijd (naar uniforme grootte gestandaardiseerde leeftijd).

6. Aangetoond werd dat, indien vergeleken in gelijkwaardige groeistadia, de allometrische groeipatronen voor het Saanen ras en het WAD ras sterk met elkaar overeenkwamen, dat de voor grootte gecorrigeerde voeropname bij de Saanen geiten hoger lag dan voor de WAD geiten, en dat de efficiëntie van voergebruik hoger was bij het Saanen ras. Ten gevolge hiervan bleken de Saanen geiten, ondanks dat ze genetisch groter waren, op gelijke leeftijd even ver te zijn ontwikkeld als de WAD geiten.

7. De schalingstheorie van Taylor biedt een doeltreffende methode om diervariatie als gevolg van verschillen in ontwikkelingsstadium en genetische grootte te onderscheiden van de overige meer diertypische variatie, en draagt daardoor bij tot een beter begrip van de biologische basis van genotypische variatie.

CURRICULUM VITAE

Nico Ogink werd geboren op 5 februari 1958 te Lierderholthuis (gem. Heino, Ov.). In 1976 behaalde hij het Gymnasium β-diploma aan het Thomas à Kempis Lyceum te Zwolle, waarna hij met de studie zoötechniek begon aan de Landbouwhogeschool te Wageningen. Tijdens zijn studie bracht hij zijn praktijktijd door in Tanzania en Kenya (1981-1982). In juli 1985 studeerde hij af met als hoofdvak Tropische Veehouderij en als bijvakken Veevoeding, Graslandkunde en Bedrijfseconomie. Hierna was hij tot begin 1986 in dienst als onderzoeksassistent bij de vakgroep Tropische Veehouderij. Na een verblijf in 1986 in Brazilië, volgde een aanstelling als assistent in opleiding bij dezelfde vakgroep over de periode 1987-1991 en voerde hij het onderzoek uit met Saanen geiten en Dwerggeiten dat beschreven is in dit proefschrift. Sinds 1991 is hij als docent verbonden aan de internationale MSc-cursus Animal Science van de Landbouwuniversiteit Wageningen.