

Patterns of muscular growth in the African Bovidae

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ABSTRACT

Grand, T.I., 1991. Patterns of muscular growth in the African Bovidae. *Appl. Anim. Behav. Sci.*, 29: 471–482.

Three types of anatomical data (body composition, regional muscle proportions, segmental distribution of body mass) are compared for neonates and physically mature individuals from 4 genera of African Bovidae. The data reveal (1) fundamental differences in the adults which correlate directly with their locomotor patterns, and (2) differences in the newborns which correlate with developmental strategy. "Lying-out" species such as Kirk's dik-dik (*Madoqua kirki*), dorcas gazelle (*Gazella dorcas*) and sable antelope (*Hippotragus niger*) possess only two-thirds of the muscle at birth than they do as adults, whereas a newborn "follower", such as the brindled gnu (*Connochaetes taurinus*), has proportionally as much muscle (40% of weight) as it has as an adult. This suggestive relationship begs further investigation. In all species muscular growth shifts the center of gravity towards the hip joint, a more optimal biomechanical position.

INTRODUCTION

Muscle dominates the mammalian body. Whereas it falls below 30% of body weight in slow-moving arboreal climbers such as sloths, it constitutes 40–50% of weight in high speed terrestrial forms such as jackrabbits, kangaroos, greyhounds and many bovids (Grand, 1977, 1978). Characteristic regional concentrations of this musculature within the limbs, back and tail correlate directly with locomotor adaptation (Grand, 1983a).

Muscle also dominates growth. For developmental as well as functional reasons, one must know the sequences and rates of growth of the major muscle groups for any given species (Hammond, 1932; Fowler, 1968; Berg and Butterfield, 1976; Grand, 1983b). Some of these characteristics are common to all mammals; others reflect taxonomic correlates (e.g. primates, artiodactyls or carnivores); still others reflect species-specific locomotor adaptation.

Three techniques of gross anatomy (body composition, regional muscular

proportions, segmental distribution of body mass) which were used to analyze Australian and new World marsupials (Grand, 1983a) and many genera of primates, edentates, rodents, and carnivores, are applied to the African Bovidae. What correlations exist between muscular proportions and locomotor adaptation, between muscular proportions and growth? In newborns with differing degrees of muscularity is there a correlation between "lying-out" and "following" behavior (Leuthold, 1977; Estes and Estes, 1979; Walther, 1979, 1984; Ralls et al., 1987)?

ANIMALS, MATERIALS AND METHODS

The 31 specimens from 4 genera came primarily from the collection of the National Zoological Park (Table 1). They represent the 4 species, Kirk's dik-dik (*Madoqua kirki*), dorcas gazelle (*Gazella dorcas*), sable antelope (*Hippotragus niger*) and brindled gnu (*Connochaetes taurinus*). Each animal was given a complete postmortem examination to establish the cause of death and to determine the state of the musculoskeletal system.

The technique of "body composition" (Grand, 1977) describes the relative proportions of skin and muscle to total body weight (% TBW). The distribution of the musculature is reflected in the proportions of each region (forelimbs, hindlimbs, back extensors) to total muscular weight (% TMW). Each section of the back extensors (cervical, thoracic, lumbar, etc.) is described as a proportion of total back muscle (% TBkW) (Grand, 1983a).

The technique of "segmentation" is modified from the original studies of all primates (Grand, 1977). The head itself is not weighed as a segment, but has to be "reconstituted" from the weights of skull, horns, mandible, brain, eyes and masticatory muscles. The weight of each segment divided by total weight gives the relative distribution of body mass.

To calculate the center of gravity, the free-body diagram of an individual

TABLE 1

Background data on specimens studied

Species	Age	Size (kg)	No. of individuals
Kirk's dik-dik	Fetal/neonatal	0.3-0.8	3
(<i>Madoqua kirki</i>)	Adult	1.7-6.3	8
Dorcas gazelle	Fetal/neonatal	0.28-1.13	3
(<i>Gazella dorcas</i>)	Adult	8.0-18.8	7
Sable antelope	Fetal/neonatal	4.0-12.8	4
(<i>Hippotragus niger</i>)	Juvenile/adult	150-157	2
Brindled gnu	Neonatal	18-25	2
(<i>Connochaetes taurinus</i>)	Adult	204-258	2

standing in lateral aspect is projected onto an x - y grid (Miller and Nelson, 1973). The major limb joints are determined as accurately as possible and along lines joining the centers of these joints, the center of mass of each segment is located. Each segment is assigned a value in % TBW. The product of moments formula locates the center of gravity of the body within the x - y coordinate system.

To contrast the centers of gravity of newborn and adult individuals, the weights of the segments in those developmental classes are substituted in the calculation. In fact, if the limb proportions are adjusted to reflect true growth, the shift in the center of gravity between newborn and adults would be even greater.

Two cautions must be observed. Firstly, this study is based upon the only direct method for the analysis of tissue composition. As the sample population is cross-sectional, a two-class comparison of fetal/neonatal, and physically, not socially or reproductively mature individuals is created. As a result of such data, the sequences and magnitudes, but not the rates, of brain and muscular growth can be represented. By contrast, Jarman (1983) traced overall growth of the body, but was not able to resolve regional patterns as detailed here. Secondly, in like manner, the wet weight of muscle represents one stage in the evaluation of muscle force. Additional data on dry weight and the cross-sectional areas of muscle, and data from individuals of other genera are necessary to verify and broaden these conclusions. Nevertheless, this is the first step in understanding mother-infant interaction within the framework of developing muscular capacity.

RESULTS

Trends from newborn to adult: Kirk's dik-dik

Body composition

Skin declines from 16% TBW at birth to 10% TBW in adulthood (Fig. 1). The musculature increases from 27% TBW at birth to 45% TBW in adulthood.

Musculature by region

At birth the hindlimb muscle represents 41% of total muscle (TMW), the forelimb 27% TMW (Fig. 2). In maturity, the disproportion increases so that the hindlimb increases to 45% TMW, while forelimb muscle falls below 22% TMW. At birth the back extensors constitute 17% TMW, at maturity they constitute > 20% TMW.

Changes also take place within the back extensors (Fig. 3). At birth the lumbar region represents 33% of total back muscle (TBkM); in maturity it increases to 45% TBkM. At birth the cervical extensor region represents almost 30% TBkM; in maturity it falls to 15% TBkM.

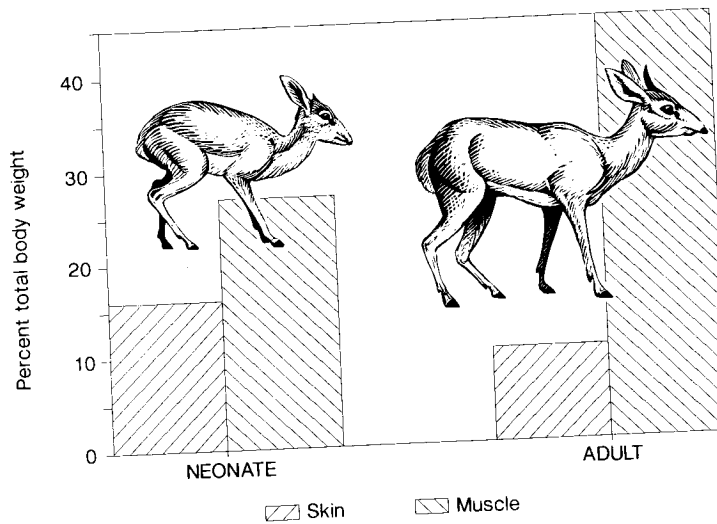


Fig. 1. Body composition in fetal/newborn and adult Kirk's dik-dik. Skin and muscle as percentages of total body weight.

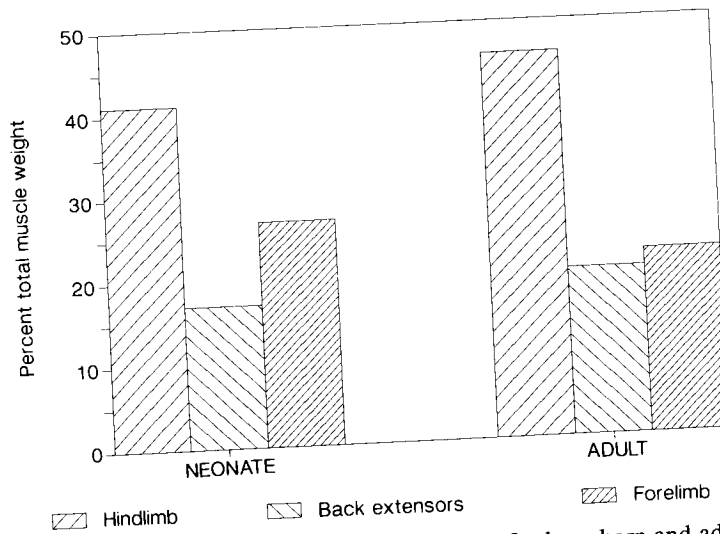


Fig. 2. Regional distribution of musculature in fetal-newborn and adult Kirk's dik-dik. Hindlimb, back extensor, and forelimb muscle as percentages of total muscle.

The segments

At birth the head constitutes > 10% TBW, each thigh ~ 5% TBW (Fig. 4). The segments below elbow and knee represent ~ 16% TBW. As the body grows to adulthood, the head falls to 4% TBW, while each thigh increases to 8% TBW. The segments below elbow and knee represent 10% TBW. As a conse-

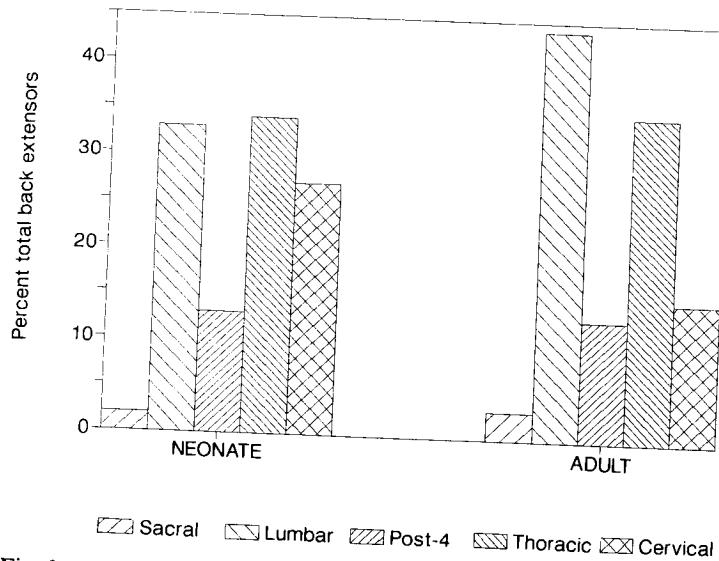


Fig. 3. Distribution of back extensor musculature in fetal/newborn and adult Kirk's dik-dik. Sacral, lumbar, posterior thoracic (Post-4), anterior thoracic (thoracic), and cervical regions as percentages of all back muscle.

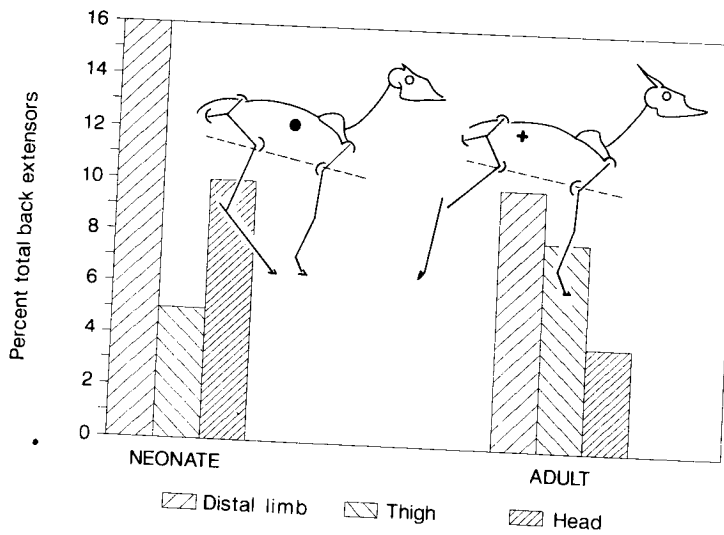


Fig. 4. Segmental distribution of body mass in fetal/newborn and adult Kirk's dik-dik. The histograms represent the relative weights of the segments distal to elbow and knee, the weight of one thigh, the weight of the head. ●, position of center of gravity in newborn; +, position of center of gravity in adult.

quence of these changes, the center of gravity shifts posteriorly and rises somewhat superiorly; that is, it moves closer to the hip joints.

Trends from newborn to adult: dorcas gazelle

The development of the dorcas gazelle is similar to that of Kirk's dik-dik. At birth, skin constitutes a relatively high proportion of body weight, but declines with maturity. Muscle at birth represents < 30% TBW, and at physical maturity 40% TBW. The head becomes relatively smaller and the thighs larger. The lumbar extensors progressively dominate the back musculature.

Trends from newborn to adult: sable antelope and brindled gnu

If one compares the 3 "lying-out" species to the "follower" (Fig. 5), those that lie out have only two-thirds of the muscle at birth that they possess as adults, while the "follower" has the same muscular proportion at birth as it does in adulthood.

Trends from small to large species

All bovids are heavily muscled (40–50% TBW), but the musculature shifts regionally between the smallest and the largest species. In Kirk's dik-dik the hindlimb muscles are twice as large as those of the forelimb (Fig. 6), whereas in the sable antelope and gnu the ratio is much closer to 1:1. The dik-dik and

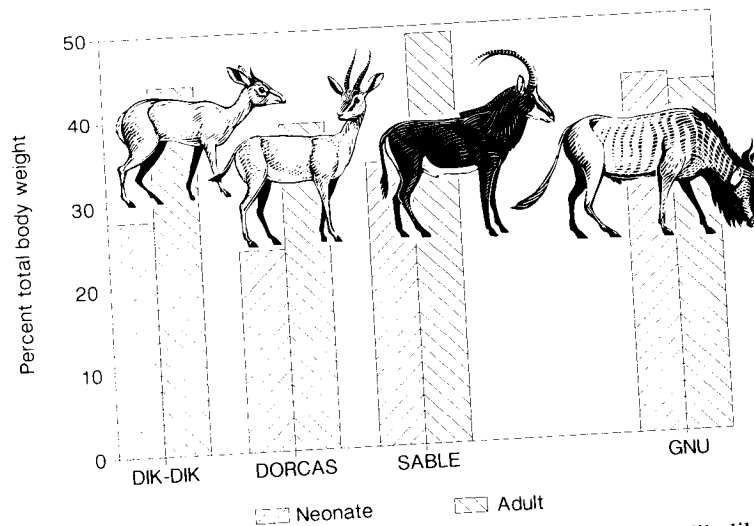


Fig. 5. Muscular proportions in fetal/newborn and adult Kirk's dik-dik, dorcas gazelle, sable antelope, and brindled gnu.

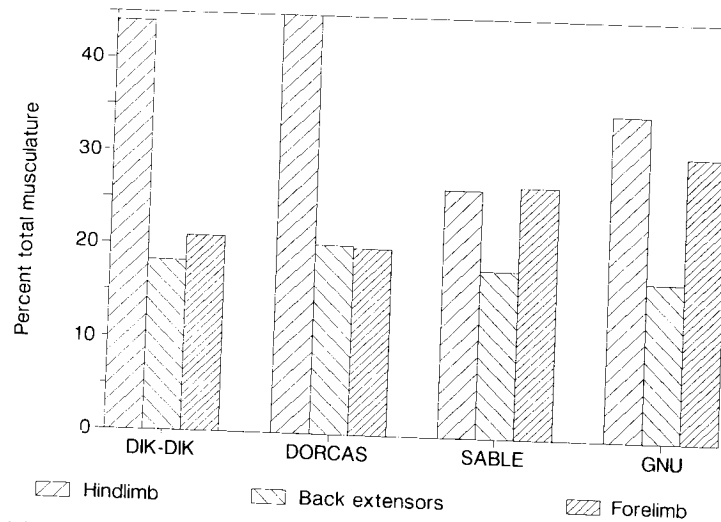


Fig. 6. Regional muscle groups as proportions of total musculature in adult Kirk's dik-dik, dorcas gazelle, sable antelope, and brindled gnu (species arranged by typical liveweight of the adults, smallest first).

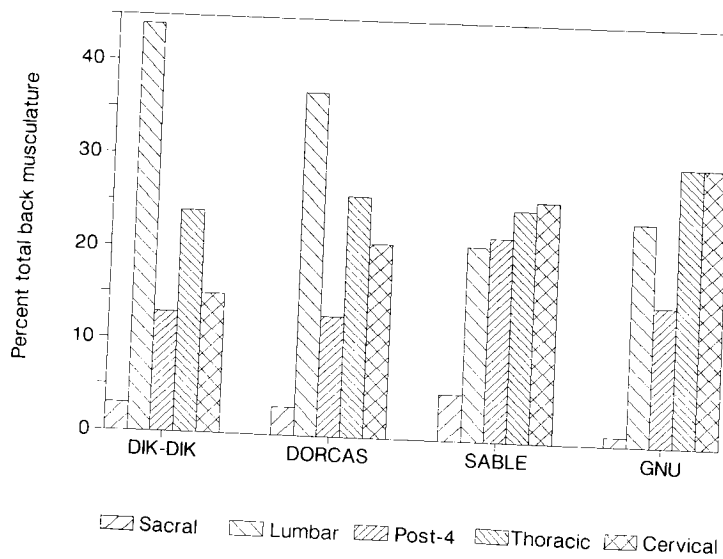


Fig. 7. Regional proportions of the back extensor muscles in adult Kirk's dik-dik, dorcas gazelle, sable antelope and brindled gnu (muscle group designations match Fig. 3).

dorcas gazelle invest the same proportion of muscle to the back extensors, but commit the highest percentages to the lumbar region (Fig. 7). The larger genera shift muscular strength into the anterior thoracic and cervical regions.

DISCUSSION

The functional anatomy of adult bovids

The locomotor adaptations of terrestrial animals tend to be more straightforward than those of arboreal species, partly because of the relative complexity of support surfaces for the latter. Arboreal pathways are curvilinear, unstable and discontinuous, a three-dimensional matrix of vines and branches, inclined in all directions. Whilst these properties are barriers to potential movement, they also offer substantial advantages. For canopy dwellers, agility replaces muscular power and explosive quickness as a technique for anti-predator avoidance. To escape, all an animal has to do is climb to an inaccessible location. Selection pressure, therefore, does not favor per se increased muscularity (an energetically expensive tissue where propulsive thrust may be dissipated in branch bending) or increased body size (larger species tend to be slower and more deliberate than smaller ones).

By contrast, the ancestral bovids committed themselves to life on the ground (a two-dimensional, resistant, continuous surface), a decision which favored muscularity and imposed few limits on body size (within 1000 kg). Small bovids such as Kirk's dik-dik and the dorcas gazelle are extremely muscular (40–45% TBW). And as it is mechanically efficient to put propulsive thrust behind the center of mass (Fokin, 1978), these species are hindlimb-dominant with the lumbar extensors representing from one-third to one-half of all back muscle. This is the muscular configuration of Gambaryan's (1974) "dorsomobile" runners. The larger bovids, represented here by the sable antelope and brindled gnu, are also heavily muscled, but possess hindlimb:forelimb ratios which are much closer to 1:1. Whereas the lumbar extensors are reduced to one-fifth of the total extensor system, the thoracic and cervical regions are increased. This is the configuration for Gambaryan's "dorsostable" runners.

Locomotor development in the bovids

Locomotor development in the bovids tends to be more straightforward than it is in the higher primates, for example, for reasons in addition to the mechanical differences between arboreal and terrestrial supports. The newborn monkey relies upon its mother for transport, clinging to her ventrum, and later riding jockey-style on her back. Only gradually does the young animal acquire the strength and range of skills (walking and running, climbing and jumping) necessary to an independent existence. By contrast, bovid newborn do not have the option of parental transport and they are potential "sitting ducks" until they can run. Thus, the primary question becomes: how

slowly or quickly does the young develop the capacity for independent movement?

"Lying-out" species versus "follower" species

Differences in the timing of muscular development are documented phenomena in precocial and altricial birds (O'Connor, 1984), primates (Grand, 1983b), red pandas (*Ailurus fulgens*) and hammerhead bats (*Hypsignathus moustrosus*) (T.I. Grand, personal observations, 1985 et seq). These data on newborn bovids suggest a strong link between the degree of maturation at birth (muscle as a percentage of body weight or the strength-to-weight ratio) and mother-offspring behavior. The "lying-out" species (Leuthold, 1977; Walther, 1979, 1984; Ralls et al., 1987) accommodate to newborn incapacity with complex behavioral interactions: immobility, crypsis, calls, etc. "Follower" newborn run with the herd soon after birth, and mother-offspring behavior develops along entirely different lines (Estes and Estes, 1979). Whatever the evolutionary interpretation of these differences, the anatomical substratum of developing strength must be considered.

Common trends in bovid development

Skin as a proportion of weight decreases with age (and increasing body size), a direct consequence of the surface-to-volume rule: as surface area increases by the square, volume increases by the cube. The head as a proportion of weight decreases as a consequence of two factors: the law of cephalocaudal development (anterior body parts grow in advance of posterior ones), the brain grows in essential advance of the musculature. The limb segments do not change uniformly either. Accelerated muscular growth increases the mass of the shoulders, hips, and thighs, whereas the distal segments become lighter.

These changes in tissues and segments in combination with those of the limb proportions cause the center of gravity to move posteriorly as well as to rise somewhat superiorly. At the same time, however, the restriction of the limb joints to the parasagittal (fore-aft) plane limits the lateral displacement of the center of gravity. (During primate growth the center of gravity shifts posteriorly, but its "cloud of probability" is far greater than in the bovids. Because of the greater ranges of joint motion, the greater proportion of body mass distal to elbows and knees, and the heavier tail, the center of gravity may travel further from the midline, even outside the body!) The limitation of the lateral displacement of the center of gravity is significant in fighting. To demonstrate their strength, individuals push against one another within those planes (the parasagittal) in which the largest muscle groups are most efficient. One animal will attack the lateral instability of an opponent, at its long, narrow base of support.

The chain of back extensors matures directly in relation to motor function. At birth, with a large head and depressed motor activity, the cervical extensors are large and the lumbar extensors small; at maturity the back extensors represent a larger proportion of total musculature. In dorsomobile cursors, such as dik-dik and dorcas gazelle, the lumbar region rises above one-third to one-half of all back muscle. This plateau of physical skill is bounded symmetrically by increasing muscle bulk after birth and its decline in old age. The 4 oldest animals in this study (10- and 11-year-old Kirk's dik-dik, 17-year-old dorcas gazelle) showed quantifiable decreases in hindlimb and lower back musculature.

Body weight as a standard value

In an abstract sense and in practice, body weight bears an enormous burden. It is one of the key attributes of a species. It is a fundamental property of the individual. It is a tool of comparative analysis. The 4 genera evaluated here fall along an axis of size from 4 to 200 kg and their components are described as proportions of total weight, as proportions of total musculature, and as proportions of the back extensors. Nevertheless, as a concrete "thing in itself" body weight has inherent limitations which ungulate biologists have long recognized. Dressed weight is one tactic by which to correct for the relative influence of the gastrointestinal tract (Lamprey, 1964). How else to estimate standing crop biomass? How else to compare species?

The problem of standard weight, however, is not restricted to ruminant biology. Physiologists normalize weight with estimates of lean body mass and fat-free mass to compensate for the effects of large, relatively inert adipose stores. Other taxa distort their body weight in still other ways. Some species "invest" 10–15% of their weight in quills (Grand and Eisenberg, 1982) or carapace for anti-predator protection. Natural selection alters body composition in divergent ways because locomotor, nutritional, anti-predator and energy storage adaptations are, to a degree, independent of one another.

Even within the Bovidae one must look past "size class" and "growth by size" (the 800-g newborn or the 4-kg adult Kirk's dik-dik, the 20-kg newborn or the 200-kg brindled gnu) to specify how an individual apportions the major fractions of body weight. In this sense, the tissue and segmental components become more important than weight as expressions of the adaptive nature of the growth process.

ACKNOWLEDGMENTS

The particular cooperation of the Departments of Zoological Research and of Pathology at the National Zoo made this study possible; in particular, Dick Montali, Chief of Pathology, Richard Freeman and Residents Peter Mann, Don Nichols, and Bruce Rideout. Karl Kranz and Barbara Lundrigan helped with a number of dissections, and Karl has continued to offer critical com-

ment and access to research materials through the Philadelphia Zoological Garden. I have been supported by a series of project grants from the Friends of the National Zoo as well as by 2 Senior Post-Doctoral Fellowships from the Wenner-Gren Foundation for Anthropological Research and the Smithsonian Institution. Dr. Fritz Walther's books and articles introduced me to the world of the bovids and provided the depth and breadth to induce me to study them.

REFERENCES

- Berg, R.T. and Butterfield, R.M., 1976. *New Concepts of Cattle Growth*. Sydney University Press, Sydney, 240 pp.
- Estes, R.D. and Estes, R.K., 1969. The birth and survival of wildebeest calves. *Z. Tierpsychol.*, 50: 45-95.
- Fokin, I., 1978. The locomotion and morphology of the locomotory organs in jerboas. Zoology Institute, Leningrad Academy of Sciences, USSR (In Russian).
- Fowler, V.R., 1968. Body development and some problems of its evaluation. In: G.A. Lodge and G.E. Lamming (Editors), *Growth and Development of Mammals*. Plenum, New York, pp. 195-211.
- Gambaryan, P.P., 1974. *How Mammals Run*. Wiley, New York, 367 pp.
- Grand, T.I., 1977. Body weight: its relation to tissue composition, segment distribution, and motor function. Part I. Interspecific comparisons. *Am. J. Phys. Anthropol.*, 47: 211-240.
- Grand, T.I., 1978. Adaptations of tissue and limb segments to facilitate moving and feeding in arboreal folivores. In: G.G. Montgomery (Editor), *The Ecology of Arboreal Folivores*. Smithsonian Institution, Washington, DC, pp. 231-241.
- Grand, T.I., 1983a. Body weight: its relationship to tissue composition, segmental distribution of mass, and motor function. Part III. The Didelphidae of French Guyana. *Aust. J. Zool.*, 31: 299-312.
- Grand, T.I., 1983b. The anatomy of growth and its relation to locomotor capacity in *Macaca*. In: J.F. Eisenberg and D.G. Kleiman (Editors), *Advances in the Study of Mammalian Behavior*. *Am. Soc. Mammal., Spec. Publ. No. 7*, pp. 5-23.
- Grand, T.I. and Eisenberg, J.F., 1982. On the affinities of the Dinomyidae. *Säugetierkd. Mitt.*, 30: 151-157.
- Hammond, J., 1932. *Growth and Development of Mutton Qualities in the Sheep*. Oliver and Boyd, London, 597 pp.
- Jarman, P., 1983. Mating system and sexual dimorphism in large, terrestrial, mammalian herbivores. *Biol. Rev.*, 58: 485-520.
- Lamprey, H.F., 1964. Estimation of the large mammal densities, biomass and energy exchange in the Tarangire Game Reserve and the Masai steppe in Tanganyika. *E. Afr. Wildl. J.*, 2: 1-46.
- Leuthold, W., 1977. *African Ungulates*. Springer, Berlin, 307 pp.
- Miller, D.I. and Nelson, R.C., 1973. *Biomechanics of Sport*. Lea and Febiger, Philadelphia, PA, 265 pp.
- O'Connor, R.J., 1984. *The Growth and Development of Birds*. Wiley, New York, 315 pp.
- Ralls, K., Lundrigan, B. and Kranz, K., 1987. Mother-young relationships in captive ungulates: behavioral changes over time. *Ethology*, 75: 1-14.
- Walther, F.R., 1979. Das Verhalten der Hornträger (Bovidae). *Handbuch der Zoologie*, 8. *Mammalia*, 54, 10 (30): 1-184.
- Walther, F.R., 1984. *Communication and Expression in Hoofed Mammals*. Indiana University Press, Bloomington, IN, 423 pp.