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Locomotion as a life history character: the contribution of anatomy

John Napier's research in primatology illuminated several aspects of motor skill and its structural and functional aspects. This study continues in Napier's tradition of emphasizing structure, function and behavior and adds a life history perspective to primate locomotion. Muscle, bone and joint properties of body segments connect individuals to their expressed locomotor behavior and underlie individual survival and reproduction. This relationship is demonstrated through three comparisons: (1) distribution of body mass across species highlights similarities and differences, and complements information based on linear measurements; (2) as an animal grows, its musculo-skeletal maturation is keyed to moving about in the external world; and (3) females are not miniature males, nor are males larger versions of females. The musculo-skeletal system has been remodeled for divergent adaptations between, and within, different species, of different ages and sexes for survival and reproduction

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John Napier and primatology

It is not an overstatement to say that John Napier's research and writings on the inter-relationships between primate locomotion, primate anatomy and the fossil record forged new directions in primatology and paleontology. He intuitively recognized that selection pressures account for shaping of the musculo-skeletal system, thereby reinforcing a form-function perspective. Napier published on a wide range of topics, from details of human walking and its possible behavioral expression inferred for the fossil record, to details of manipulative abilities expressed in power and precision grips, and their possible expression among early hominids.

Napier's perspective, as well as the details of his research, contributed to my research in a number of ways, particularly in his vision that locomotor behavior is an important and central focus of primatology. In addition, he incorporated the natural environment: primates move within a three-dimensional world (Napier, 1962). I first drew on his perspective, as well as on the results of his investigations, during study for my doctoral dissertation on human bipedality (Napier, 1964).

Taking John Napier's approach further, in this paper I concentrate upon anatomical methods that contribute to the study of locomotor adaptation, development and sex differences. Locomotion is fundamental to foraging and feeding and to predator avoidance, to mating and caring for offspring. Locomotion, therefore, compels consideration of the whole animal throughout its life cycle. This tribute to John Napier indicates how locomotion is central to an individual's ability to survive, to mate and to ensure the survival of its offspring, and therefore to the broader framework of life history theory and reproductive success.

Locomotion and life history

This paper develops two themes: my research methods and topics, and my pursuit of a theoretical framework for life history phenomena. Since the middle 1960s, through dissections of whole animals and studies of skeletal biology, I have been concerned with anatomical

methods. How is it possible to compare animals which differ in body weight between species, ages and sexes? What kinds of information can be derived from the skeleton? In what ways is locomotor adaptation reflected in bones?

Ted Grand's research on primate anatomy and body weight (e.g., 1977*a*, 1977*b*, 1983, 1990) have been influential both methodologically and conceptually. When whole animals are dissected and body parts weighed, it is possible to determine: (a) tissue composition within body segments and throughout the body; and (b) the distribution of body weight to the various body segments (e.g., head; trunk; forelimbs, consisting of arm, forearm, hand; hindlimbs, consisting of thigh, leg, foot). Such methodology reveals that 60–80% of an animal's body weight (skin, muscles, bones) is devoted to the locomotor system (e.g., Grand, 1977*a*, 1977*b*) and provides a valuable supplement to linear measurements.

Added to laboratory work is research on Gombe chimpanzees, carried out in collaboration with Mary Ellen Morbeck (Morbeck & Zihlman, 1988, 1989; Zihlman *et al.*, 1990). As a result of the long-term behavioral studies on these animals by Jane Goodall and colleagues (e.g., Goodall, 1986), we are able to broaden research on the skeletal biology to include specific dimensions of individual life history. The skeletons of individual animals known throughout their lives provide the opportunity to connect anatomy to events in the animals' lives and to begin to see the interplay between locomotion, development, disease and social life.

The expanded time scale over individual lives into multiple generations, as Goodall (1986), Altmann (1980) and many other long-term field researchers reveal, encourages the incorporation of anatomy and locomotion into the broader theoretical framework of individuals, generations and species. Life history studies, involving both demography and individuals, are not easy to carry out. Primates, like other socially complex mammalian species, live long lives in multi-generational groups (Eisenberg, 1973). Longer survival time prior to physical and social maturity increases social plasticity of individuals and their social groups, and in turn increases their potential for problem-solving (Mason, 1979; Grand, 1983; Morbeck, n.d.). How might the musculo-skeletal system and expressed behavior be interpreted within such a framework?

Life history studies most often stress reproductive characters which reflect the tempo of life stages (e.g., gestation length, age at weaning, age at first reproduction) and determine the frequency and number of births and potential costs of reproduction, and thus, reproductive success (e.g., Altmann, 1983; Harvey *et al.*, 1987). Other life history characters promote survival and so *allow* successful mating and adequate care of offspring (Morbeck, 1991; Zihlman *et al.*, 1990). Both survival to the age of reproduction and the individual's survival while reproducing are important (e.g., Altmann, 1980). Because the life history framework most often stresses reproductive parameters, features that contribute to survival have been discussed less extensively.

However, life history studies must include the individual throughout its life course; they must also explore the implications of individuals as members of social groups and populations (e.g., Cheney *et al.*, 1988; Altmann *et al.*, 1988). Each stage of life is subject to natural selection, and thus, the entire life history of an organism evolves (Mason, 1979). Life history adaptations include both survival and reproduction (e.g., Morbeck, n.d., 1991; Zihlman *et al.*, 1990).

Locomotion intersects with other life history characters and therefore provides the means to focus on individuals through all stages of their life course, to look "inside the animal" at its muscles and bones, and to look "outside the animal" to the social group, the physical

environment, population and species (Morbeck, 1991). Locomotor behavior and its associated tissues provide one way to approach the study of different levels of biological-behavioral organization. Consequently, comparative anatomical studies have a great deal to contribute to understanding survival features and, therefore, life history at the individual as well as the species level.

Because locomotion is so integrated with the whole animal, it becomes a central aspect of animals' time and energy budgets, and involves postural, locomotor and manipulative behaviors for feeding, traveling, socializing and resting (e.g., Coehlo, 1986; Dunbar & Dunbar, 1989; Mitani, 1989). Female primates carry their young, so that survival while mating and survival while rearing offspring are critical, and the locomotor system is involved in both. For male primates, Alison Richard provides an example in *Propithecus* (Richard, 1992)—males chasing other males may be more important than fighting in competition for females, and it is helpful if the winner is not too exhausted to mate.

Thus, the impact of locomotor capacity differs for the various age classes in terms of survival, mating and rearing offspring; adult females, adult males, infants and juveniles all have different problems to solve at their respective life stage. Unless primates are the focus of life history studies, this point may be overlooked.

Mammals, primates and life history

Primates share a similar life pattern with other mammals: they are born, they grow to maturity, they reproduce, they die. Lactation of adult females and suckling of infants makes possible the growth pattern of young mammals and consequently, the pattern of life stages (Pond, 1977). Although life is continuous, each stage from infancy through old age varies in duration across the mammals.

After giving birth, female mammals accommodate the demands of lactation while maintaining their own energy balance in a variety of species-specific ways. Female elephant seals lie at one end of the mammalian pattern (LeBoeuf & Reiter, 1988). Lactating elephant seal females, unlike other mammalian females, conserve energy during lactation by sharply curtailing locomotor activities. Gravid females come ashore, give birth, lie on the beach, and produce milk; the young suckles for about a month. During this time, the females do not go to sea to feed and move little around the rookery. When an infant is weaned, the female comes into estrus, mates, and returns to the sea. Females transfer sufficient energy and nutrients to sustain the maintenance and development of pups for at least the first $3\frac{1}{2}$ months of life (Ortiz *et al.*, 1984; Costa *et al.*, 1986).

Some of the ungulates, such as wildebeest females and young, illustrate a contrasting pattern of locomotor mobility. In the Serengeti ecosystem, energy expended in migrating is quite large, but the resulting increase in food intake compensates (Pennycuick, 1979). Young wildebeest, within an hour after birth, are capable of effective independent locomotion, both to gain protection from predators by following close to mother and for migration. The seasonal movements of lactating and late pregnancy wildebeest females in the Serengeti ecosystem are related to grass mineral content, so that their direction of travel is influenced by their nutritional requirements (McNaughton, 1990). Unlike elephant seals, female wildebeest rely on mobility to travel long distances to obtain proper grazing. For this species, locomotion plays a different role in survival and energy balance for both females and offspring.

Table 1 **Locomotor anatomy: hands and feet**

Mammal	Percent total body weight ¹	
	Hands	Feet
<i>Perodicticus</i>	2.4	3.0
<i>Galago</i>	1.4	3.0
<i>Ateles</i>	1.6	2.8
<i>Alouatta</i>	2.0	3.4
<i>Cebus</i>	1.8	3.2
<i>Macaca</i>	1.4	2.4
<i>Symphalangus</i> ♀	2.8	2.8
<i>Pongo</i> ♀	2.8	3.5
<i>Pan</i> ♀	2.0	2.8
<i>Homo</i> ♀	1.1	2.7
<i>Tupaia</i>	0.4	1.4
<i>Canis</i>	1.0	1.2
<i>Macropus</i>	0.4	2.8

¹Percent total body weight, rounded off to nearest tenth.

Data from Grand 1976, 1977a; *Pongo*, Morbeck & Zihlman, 1988; *Symphalangus* and *Pan paniscus*, Zihlman 1984 and unpublished data; *Homo*, Clarys & Marfell-Jones, 1986.

Primates (especially catarrhines) present yet another pattern that differs considerably from most other mammals. From the infant's point of view, it is dependent on the mother for nourishment, protection *and* transportation. While suckling and getting a free ride, the infant is physically growing and developing motor and social skills for later independent survival. The mother, on the other hand, lactates for a long period of time and moves herself and her infant until weaned around the home range. In addition to energy for milk production, she expends energy carrying the additional weight of the infant through the forest canopy or on the ground. These combined energy costs require lactating females to compensate by modifying some combination of travel, feeding time, dietary composition or social life (e.g., Altmann, 1980; Gautier-Hion, 1980; Cords, 1986; Dunbar & Dunbar, 1989). Consequently, compared to males of the same species, the time and energy budgets of female primates vary among primate species.

Primate locomotor anatomy: case studies

Interspecific comparison

Primate locomotion emerged from a small-bodied insectivorous mammal, perhaps with the capabilities of tree shrews (Jenkins, 1974), to develop an adaptation of climbing by grasping (Washburn, 1951). Primate hands and feet share a number of features: long straight digits equipped with nails and sensory pads, opposable pollex and hallux; and well developed palms and soles (well illustrated in Schultz, 1969). In addition to these external features, relative mass reflects the importance of strong mobile grasping hands and feet for locomotion (Table 1).

Table 2 Locomotor anatomy: forelimbs, hindlimbs and tail

Mammal	Percent total body weight ¹		
	Forelimbs	Hindlimbs	Tail
<i>Perodicticus</i>	12	14	0.4
<i>Galago</i>	9	23	3.0
<i>Ateles</i>	14	24	8.0
<i>Alouatta</i>	10	16	6.0
<i>Cebus</i>	12	20	6.0
<i>Macaca</i>	13	25	0.5
<i>Symphalangus</i> ♀	20	18	—
<i>Pongo</i> ♀	16	18	—
<i>Pan</i> ♀	16	24	—
<i>Homo</i> ♀	9	38	—
<i>Tupaia</i>	4	17	2.5
<i>Canis</i>	9	20	0.4
<i>Macropus</i>	3	31	4.0

¹Percent total body weight rounded off to nearest whole number.

Sources as in Table 1.

In a sample of primate species whose body weight varies from the galago (about 1 kg) to the larger orang-utans (30–80 kg), hands and feet comprise between 1.4–3.5% of total body weight; at least a third of the weight is muscle. In contrast, the hands and feet of the dog (*Canis*) are only 1.0–1.4% and consist almost entirely of skin and bone (Grand, 1977a).

Primate hands are less massive than the feet. They vary relative to body weight from lightest of all in human females (1.1%) without locomotor function, to the galago (1.4%), a skilled leaper and hopper. At the heavier end of the spectrum, hands are 2.4% in the potto (*Perodicticus*), a slow climber, to the quadrumanal female orang-utan (2.8%). In contrast, tree shrew hands are only 0.4% of total body weight, even though they do use their hands for some manipulation as well as weightbearing. Feet are more massive than the hands and range from 2.4% in the macaque, to 3.5% in female orang-utans. Only the feet of the specialized hopping kangaroo (*Macropus*) lie within the primate range.

Primate locomotion is dominated by the hindlimb (Napier & Walker, 1967; Kimura *et al.*, 1979); the variations on this theme range from the extreme vertical clingers and leapers, illustrated by galagos, and bipedal humans, to the quadrupedal macaques (Table 2). Furthermore, the distribution of body weight to the forelimbs, hindlimbs and tail, reflect the locomotor range and potential of various primate species. For example, *Perodicticus*, as a slow climber has heavy hands and feet, with forelimbs and hindlimbs nearly equal in weight; it relies on its stealth and pincer, but non-propulsive, hindlimbs. The galago, in contrast, has 26% of body weight in its hindlimbs and tail, which highlights its jumping and leaping abilities.

The reliance on the tail of the large-bodied New World monkeys, such as *Alouatta* and *Ateles*, is reflected in its massive size—6 and 8%, respectively, and with combined hindlimb and tail mass of 22–32% of total body weight (Grand, 1977a). These percentages illustrate the investment of body weight in the lower part of the body of these species. *Cebus* and *Macaca* are more typically quadrupedal and show differentiation of propulsion of hindlimbs and hindlimb domination.

Table 3 Primate limbs: volume and length

Primate	Relative weight		Intermembral index ¹
	Forelimbs	Hindlimbs	
<i>Perodicticus</i>	12	14	88
<i>Galago</i>	9	23	62
<i>Ateles</i>	14	24	105
<i>Alouatta</i>	10	16	98
<i>Cebus</i>	12	20	81
<i>Macaca</i>	13	25	89
<i>Symphalangus</i> ♀	20	18	148
<i>Pongo</i> ♀	16	18	137
<i>Pan</i> ♀	16	24	102
<i>Homo</i> ♀	9	38	75
<i>Tupaia</i>	4	17	80

Sources as in Table 1.

¹Intermembral Index: Napier & Napier, 1967; Morbeck, 1972; Morbeck & Zihlman, 1988, 1989.

Forelimbs of the two hominoids (*Pongo* and *Pan*) shown in Table 2 are 16% of total body weight and emphasize their function in hanging and climbing; *Ateles* shows some convergence here with forelimbs (14%), in a species where hanging and progressing below branches (while supported by the tail) is a significant posture and locomotor behavior. However, these species are far surpassed by the siamang (*Symphalangus*) whose forelimbs are 20% of body weight. This high relative weight reflects an emphasis on the forelimbs during locomotion, an activity with agile and acrobatic movements through an exclusively arboreal habitat.

Linear dimensions are also used to express adaptation across species, and they tell another part of the locomotor story. The addition of relative masses clarifies the variation observed in body proportions (Table 3). For example, in intermembral index as in segmental mass, *Ateles* (spider monkey) converges with *Pan* and reflects the emphasis in both species on suspensory locomotion. *Perodicticus* and *Macaca* have similar intermembral indices (88 and 89, respectively), but very different forelimb and hindlimb weights. The high relative weight of the hindlimb in *Macaca* (25%), nearly twice their forelimbs (13%), is significantly greater than that of *Perodicticus* (14%). This difference in mass reflects the propulsive function of the macaque's hindlimb and the significant muscularity of the thigh (Grand, 1983).

The comparison of *Perodicticus* and *Pongo* offers another perspective. Their forelimb-hindlimb proportions are similar, 12/14 vs. 16/18, respectively, yet their intermembral indices are notably different, 88 vs. 137. Their similar masses reflect similar locomotor activities that emphasize rotation of the joints in traveling through the forest canopy, rather than propulsion. The intermembral indices reflect the evolutionary history of orang-utans as hominoids, where the forelimbs function in hanging and reaching, whereas the potto's intermembral index is similar to that of other more typical quadrupeds.

Homo, when compared to other hominoids, has long upper limbs relative to trunk length (Schultz, 1969), but has a low rather than high intermembral index. The low forelimb mass, as with the hands, converges in *Homo* (9%) and *Galago* (9%) and illustrates the shift away

Table 4 **Body segments in fetal and adult male *Macaca mulatta***

Body segment	Percent total body weight ¹	
	Fetal (250 g)	Adult (6–12 kg)
Forelimbs	12.0	13.0
One side:		
Arm	2.2	3.4
Forearm	2.3	2.3
Hand	1.3	0.6
Hindlimbs	16.0	25.0
One side:		
Thigh	3.7	8.2
Leg	2.3	3.0
Foot	1.9	1.2
Head/trunk	72.0	62.0
Head	25.0	7.0

¹Rounded off to nearest tenth.
Modified from Grand 1977b, 1983.

from weight-bearing in both, and away from all locomotor function in *Homo*. The segmental data, as for the intermembral indices, also suggest a minimum of three separate postcranial patterns among the higher primates (Aiello, 1984).

Locomotor development: Macaca mulatta

During development, tissue composition and body proportions change in response to the acquisition of independent and skilled locomotor and manipulative behavior. The changes can be inferred by comparing fetal term macaque infants with adults in their (a) tissue composition and (b) body segments (Grand, 1977b, 1983).

An infant macaque clings to its mother for transport; early on, hands manipulate and explore the environment. As the infant grows and develops an independent locomotor mechanism, the weight shifts from the trunk and head to the hindlimbs.

Table 4 shows body segments in the fetal and adult macaques. Relative to body weight, the forelimbs as a whole change little in mass. The infant's hand is about twice as heavy relatively as that of the adult and the arm two-thirds as heavy. However, these segments grow differentially; the upper arm and shoulder musculature grow significantly, thus dwarfing the hand.

As brain growth reaches its adult size and the musculo-skeleton increases, the head proportion decreases from 25% to 7% of total body weight, from infant to adult. The hindlimb undergoes a significant increase, from 16% to 25% of body weight. The foot decreases much less than the hand. The most pronounced increase is in the thigh. The center of gravity moves posteriorly, as brain growth ceases and adult body weight and composition is reached much later (Grand, 1983).

This shift to locomotor independence is also reflected in relative proportions of skin, muscle and bone tissues (Table 5). The most pronounced difference is in the increase of muscle in functional blocks, from 25% of body weight to 43%. Thus, the process of going from birth to adulthood entails a reorganization of body weight and, at the same time, an infant primate

Table 5 Tissue composition in fetal and adult male *Macaca*

Tissue	Percent total body weight ¹	
	Fetal	Adult
Skin	14	12
Muscle	25	43
Bone	20	15

¹Rounded off to nearest whole number.
Modified from Grand 1977*b*, 1983.

Table 6 Orang-utan body segments: adult female and male

Body segment	Percent total body weight	
	Adult female	Adult male
Head	7	7
Trunk/hip	59	64
Forelimbs	16	17
Hand	1.4	1.4
Hindlimbs	18	12
Foot	1.8	1.2
Leg	2.4	1.7
Thigh	4.7	3.1

From Morbeck 1972, Morbeck & Zihlman, 1988.

is transformed from locomotor appendages with powerful gripping abilities to propulsive locomotor independence.

Sex differences: orang-utan case study

The final example illustrates variation within a species, between female and male orang-utans. One of the first indications that female and male primates differed by more than body weight came from Napier & Napier (1967). They reported that among New World prehensile-tail monkeys, tail length varied less between females and males than did body weight. For example, although howler monkey females are 77–81% of male body weight, female tail length is only 93% of that of males. This small, but important, detail suggested that female bodies are not just smaller versions of males, or that males are not necessarily larger versions of females. What other features might differ between the sexes and what functional reasons might account for them?

The answer to this question can be approached by this methodology, which allows anatomical comparisons even with marked difference in body weight. I have maintained for some time that morphological differences between female and male primates, including hominids, consists of a mosaic of features that may vary independently (Zihlman, 1976,

1981). Each species may have its own distinctive pattern, e.g., *Pan troglodytes* and *Pan paniscus* (Zihlman & Cramer, 1978). This mosaic of anatomical difference is well illustrated by orang-utans; females are not simply smaller versions of males (Morbeck & Zihlman, 1988).

Table 6 summarizes orang-utan limited body segment data.* Although the female and male are similar in relative head (7%) and forelimb (16% vs. 17%) weights, the hindlimbs are distinct (18% vs. 12%). However, in intermembral index there is little difference in means of males and females (calculated from Morbeck, 1972, and unpublished data). This might indicate that linear limb proportions is a species specific trait (e.g., Morbeck & Zihlman, 1989) whereas relative mass can vary between the sexes.

Field studies on orang-utan posture, locomotion, feeding and travelling indicate that females and males differ in-travel and feeding time, and in forest level and locomotor methods (Sugardjito, 1982; Sugardjito & van Hooff, 1986; Cant, 1987*a,b*; Mitani, 1989; Galdikas, 1988). For example, males do more branch swaying as a means to travel horizontally through the canopy, whereas females engage in more quadrumanous "clambering" and travel and sleep in higher levels. When carrying an infant, however, females travel in the lower levels, as do the males.

The particular weight distribution to the limbs which is effective for females is apparently not effective for the much larger males. The combination of field data and anatomical data indicate that locomotion differs between female and male orang-utans as part of differences in what they need to do to survive, reproduce and care for dependent young. The emphasis on the whole animal that attempts not only to interrelate functional complexes but to take into account its behavioral expression in a free-ranging situation would have been appreciated by John Napier.

Summary

Napier directed attention to the importance of primate locomotion, that it must take into account structure and function. From films of primates moving under free-ranging conditions, he documented what animals actually do. The anatomical findings presented here follow in the example set by John Napier, who focused on whole animals; this adds another dimension to individual anatomy as the basis for locomotion and a perspective of sex differences in morphology that goes beyond canine tooth size or body weight. Locomotor behavior is an important part of survival, of mating and rearing offspring, especially for female primates. By looking across species, at different age and both sexes, we can begin to appreciate the variation.

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*It is important to note that these findings are based on the complete dissection of only two animals. This is indeed a small sample and must be considered preliminary. However, the results are of interest and perhaps will promote further investigation. The difficulties of obtaining rare and complete specimens for detailed dissection are obvious.

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