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Gaits in mammals

ANNE INNIS DAGG

Research Assistant Professor, Department of Biology, University of Waterloo, Waterloo, Ontario, Canada

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INTRODUCTION

In recent years there has been a great deal of published work on the movements of various mammals, in particular, studies on the bone morphology and range of movements of joints, the muscle structure and places of muscle attachment, the physiology of muscle performance, the peculiarities of species as mechanical systems and the specific leg movements in the gaits of some common mammals—monkeys, cheetahs, dogs, horses and pecoran species. No comprehensive work on the gaits of mammals has been undertaken that relates these movements with the phylogeny, anatomy, and habitat of the mammals. This review attempts to do this, using observations in the literature and data gathered during 13 years of study of movements in mammals by the author.

The difficulty in determining the actual gaits of a species is far more difficult than one might imagine. Even in bears there is confusion. Harington (1970) for example writes that Polar bears only walk and gallop; Van Wormer (1966) states that Black bears move with a walk, running walk or gallop, whereas Osteen (1966) claims that bears also trot and pace. All of these authors have studied bears in depth, yet even they are not agreed on how they move. If the gaits of large animals like bears have not yet been established with certainty, how much less is known of small mammals whose legs move far faster.

Another problem is the ambiguity of words used to describe gaits. How can one characterize the 'trotlike run' or 'semi-trot-gallop' of a Common shrew? (Jackson, 1961). *Running* usually means galloping, but it also has been used to mean pacing, trotting or bounding. Mortimer

(1963) notes that the Spotted-necked otter runs about 4 feet per second, but gallops about 6 feet per second, whereas Taylor (1970) distinguishes three fast gaits in viverrids, trotting, running and galloping.

Another source of ambiguity is the use of the word *rack*. Although Harrison Matthews (1969) follows Muybridge (1899) in equating the rack with the pace, Howell (1944) says it is the same as both the amble and the running walk. Horse trainers meanwhile use rack to define the showy, man-taught, artificial gait which is the fifth of five-gaited show horses (Crabtree, 1962). In this fast, tiring, collected gait each foot strikes the ground separately and at regular intervals. *Amble* too is an ambiguous word better not used. It has been applied for centuries to the walk of the giraffe (Mongez, 1827; Bourlière, 1956), but it has also been used for other gaits, among them the rapid gait of hippos (Slijper, 1946), the fast or running walk (Harrison Matthews, 1969) and the much faster pace of the camel (Magne de la Croix, 1936).

Because of the above problems, the gaits of some species are queried in Table 1—an asterisk indicates that the animals possess the gait in question—and there is a possibility of error in even unqueried gaits. Despite the lack of information on gaits, I have compiled this study in part so attention will be focussed on the gaits of animals being studied. Ethologists should not have to admit they do not know how an animal moves after they have watched the species for years.

TERMS OF REFERENCE

In order to make a useful and cohesive study, I have had to eliminate various data because they were incomplete, confusing, or of doubtful validity. Specifically, I adhered to the following criteria:

(1) Domestic animals are not emphasized in this paper, because they have been bred by man for adaptations that are often unnatural. Whereas in most mammals the pelvic bones lie at 45°, they are nearly horizontal in the cow, as this position gives the best support to the heavy udders which are suspended below them (Putnam, 1947).

(2) Only adult mammals are discussed, because these are presumed to be the individuals most adapted to their environment. Although human children crawl on all fours, the human gait is considered to be a bipedal one only.

(3) In part because the words used for gaits are inexact, so that it is sometimes impossible to interpret what movements an animal actually uses, many uncommon mammalian families are not discussed here. In the Tenrecidae there are ten genera with a variety of different shapes and gaits (Eisenberg & Gould, 1970) but these animals have not been well-enough studied yet to make useful correlations between anatomy, habitat and locomotion feasible. Similarly, virtually no work has been done on the gaits of small mammals such as rodents and insectivores, with the exception of desert species which hop or bound (Bartholomew & Caswell, 1951; Bartholomew & Cary, 1954; Marlow, 1969). There is no reason to believe that there is not a variety of gaits present as great as that in large mammals or even greater (Hildebrand, 1968). Hamilton (1963) for example compares the leaping gait of Deer mice with the very different trotting gait of Wood voles and shrews.

(4) Speeds of animals are not considered here, as they have been compiled often before (Howell, 1944; Bourlière, 1956). Also, the speeds are often taken from the literature or reported from casual observations that may be grossly inaccurate. Guggisberg (1961: 107) for example quotes maximum speeds for the lion of from 23·5 to 70 miles an hour and for the cheetah of from 44 to 90 miles an hour.

(5) Abnormal gaits have not been discussed because so few have been documented. However, this will be a fruitful field in the future. Grogan (1951) has already reported on how changes in gait in horses can reveal a number of pathological problems. These could include not only joint or muscle disabilities, but changes caused by drugs (as giraffe injected with M99, which take distinctive short steps, J. B. Foster, personal communication).

(6) The front and hind legs are assumed to move at the same rate, which is almost universally true for mammals. One exception is in the Sea otter—'When hurrying there is sometimes no co-ordination as the short front legs are moved rapidly, together or alternately, and the hind legs are moved more slowly.' (Harris, 1968: 256). Walking primates, too, may twist their bodies in such a way that the front legs move asymmetrically (Hildebrand, 1967).

(7) Gaits must be used significantly to be included here. For example Ewer (1963) reports that the short legs of meerkats make trotting an inefficient gait for them, so that it is only used briefly in this species during the transition from walking to galloping. It is thus not counted as one of this species' regular gaits.

(8) Although many species have distinctive gaits that identify them readily, these differences are not necessarily discussed here. Thus the swift Prairie hares can be distinguished because the Whitetail jackrabbit *Lepus townsendi* runs like a deer, with high, long bounds, whereas the Blacktail jackrabbit *Lepus californicus* has shorter quicker bounds much more regularly punctuated with high spy-hops which allow it to see over tall grass as it runs (Seton, 1953). Hares in general, bound for long distances while rabbits and pikas are more likely to dodge and scuttle to shelter. Since these different movements are made with the same basic gaits, they will not be distinguished here.

METHOD

Table 1 was compiled to facilitate the comparison of the gaits of various mammals to their morphology and habitat. Only those species whose gaits were well-known were included. The various characteristics of the mammals were categorized in the following way:

(1) Weight (Column 1)
- 1 Under 0·5 kg
- 2 0·5–2·5 kg
- 3 2·5–10 kg.
- 4 10–25 kg
- 5 25–250 kg
- 6 250–750 kg
- 7 over 750 kg

(2) Tail Length (Column 2)
- – No tail
- S Short—less than 1/6 head and body length
- M Medium—greater than 1/6 but less than 1/2 head and body length
- L Long—between 1/2 and 1 head and body length
- VL Very Long—greater than head and body length

(3) Slope of Back (Column 3)
- 1 Back more or less flat
- 2 Back sloping down from head
- 3 Back sloping down to head
- 4 Back distinctly humped in middle

(4) Body Shape (Column 4)

Six categories were used, one for mammals with enlarged hind legs like kangaroos and Kangaroo mice and five for quadrupedally-moving mammals.

$$\text{The formula } \frac{\text{Shoulder height}}{\text{Trunk length}} \times 10$$

was used on side view photographs of each species, so that the relative leg lengths of the mammals could be compared. The categories were:

Table 1

Gaits, measurements and habitat of various mammals

	Weight 1	Tail 2	Back slope 3	Shape 4	Walk 5	Walk using tail 6	Running walk 7	Trot 8	Pace 9	Gallop 10	Bound 11	Ricochet 12	Alternate hind 13	Stott 14	Climb trees 15	Stand 16	Habitat 17	Reference for gaits 18
Ornithorhynchus (Platypus)	2	M	1	D	*		*			no							1	Burrell, 1927
Didelphis marsupialis (Opossum)	3	L	1	D	*			*		no					*		2	McManus, 1970; Hartman, 1952
Antechinomys (Marsupial jerboa)	1	VL	—	X	?						*					*	3	Marlow, 1969
Sminthopsis	1	L	—	—	•					*	*				*	*	2	Ewer, 1968
Lasiorhinus (Wombats)	5	S	1	C	*					*							2	Wünschmann, 1966
Setonix (Quokka)	3	L		X		*					*	*				*	2	Windsor & Dagg, 1971
Dendrolagus (Tree kangaroo)	3	VL		X		*					*	*				*	4	Windsor & Dagg, 1971
Macropodinae (Wallabies)	3,4,5	L		X		•						*				*	4	Windsor & Dagg, 1971
Macropus (Kangaroo)	5	L		X		*						*				*	2	Windsor & Dagg, 1971
Sorex (Shrew)	1	L	1	(D)	•			*		*					*		4	Reed, 1951
Erinaceus (Hedgehog)	2	S	1	D	*			*							*		2	Ennion & Tinbergen, 1968
Lemur catta (Ring-tailed lemur)	2	VL	3	B	*		*			*		*			*	*	2	Jolly, 1966; Hildebrand, 1967
Propithecus (Sifaka)	4	VL	—	—	no							*	*		*	*	5	Eimerl & De Vore, 1965; Jolly, 1966
Lagothrix (Woolly monkey)	3	VL	—	A	•								*		*	*	5	Schultz, 1969
Ateles (Spider monkey)	3	VL	—	A	*								*		*	*	5	Schultz, 1969
Saimiri (Squirrel monkey)	2	VL	—	—	*					*			(*)		*	*	5	Rosenblum & Cooper, 1968
Cebus capucinus (Capuchin monkey)	3	VL	—	—	*					•			*		*	*	5	Lessertisseur & Petit-Maire, 1972
Presbytis entellus (Gray langur)	4	VL	—	—	*					•					*	*	5	Ripley, 1967

Erythrocebus patas (Patas monkey)	4	VL	—	A	*			*				*	*	2	
Macacus speciosus (Stump-tailed macaque)	3	S	—	B	*			*			*	*	*	5	Bertrand, 1969
Papio (Baboons)	5	S–L	2	B	*			*				*	*	2	
Hylobatinae (Gibbons & Siamangs)	3	—	—	(A)	(*)						*	*	*	5	Hildebrand, 1967
Pongo (Orang utan)	5	—	—	—	*						(*)	*	*	5	Schultz, 1969
Pan (Chimpanzee)	5	—	2	A	*			*			*	*	*	5,4	Reynolds, 1965; Goodall, 1965
Gorilla (Gorilla)	5	—	2	A	*			*			*	*	*	4	Eimerl & De Vore, 1965
Homo (Man)	5	—	—	—	no						*	*	*	2	
Myrmecophaga (Giant anteater)	4	L	1	C	*			*						2	
Bradypodidae (Sloths)	3	–,S	—	B	no							*		5	Tirler, 1966
Dasypus (Armadillo)	3	L	4	D	*		?	*					*	2	Fitch, *et al.*, 1952; Seton, 1953
Manis (Pangolins)	3,4,5	L	4	B,C	*	*		*			*		*	2	Vincent, 1964; Kingdon, 1971
Ochotona (Pika)	1	S	1	C	?				*					2	Millar, personal communication
Sylvilagus (Rabbits)	2	S	—	X	(*)				*					4	
Lepus groenlandicus and *L. arcticus* (Northern hares)	3	S	—	X	?				*	*				6	
Other lepids	3	S	—	X	(*)				*	(*)				6	
Glaucomys (Flying squirrels)	1	L	—	C	*				*			*	*	4	
Sciurids (from West Africa)	1	L	—	C,D	*				*			*	*	4	Rosevear, 1969
Sciurus (Squirrels)	1	L	—	D	*				*			*	*	4	
Tam·asciurus (Red squirrels)	1	L	—	C,D	*				*			*	*	4	
Tamias (Chipmunk)	1	L	—	D	*				*			*	*	4	Allen, 1938
Marmota (Woodchuck)	3	L	—	D	*		*	*				*	*	6	Schoonmaker, 1966
Cynomys (Prairie dog)	2	M	—	C	•			*					*	6	
Spermophilus richardsoni (Richardson's ground squirrel)	2	S	—	D	*				*				*	6	Quanstrom, 1971
Spermophilus columbianus (Columbian ground squirrel)	2	S	—	D	*				*			(*)	*	6	Steiner, 1970

Table 1—*Gaits, measurements and habitat of various mammals—continued*

	Weight 1	Tail 2	Back slope 3	Shape 4	Walk 5	Walk using tail 6	Running walk 7	Trot 8	Pace 9	Gallop 10	Bound 11	Ricochet 12	Alternate hind 13	Stott 14	Climb trees 15	Stand 16	Habitat 17	Reference for gaits 18
Microdipodops (Kangaroo mice)	1	VL	—	X							*	●				*	3	Bartholomew & Cary, 1954
Perognathus (Pocket mice)	1	L,VL	—	—	*						*					*	3	Bartholomew & Cary, 1954
Dipodomys (Kangaroo rats)	1	VL	—	X		*						*	*		*	*	3	Bartholomew & Caswell, 1951
Castor (Beaver)	5	M	—	—	*			no		*						*	1	Warren, 1927
Pedetes (Spring hare)	3	L	—	X							*	*				*	3	
Microtus (Field mice)	1	M	—	—	*			*		*							6	
Notomys	1	VL	—	X	(*)							*				*	3	Marlow, 1969
Rattus (Rats)	1	L,VL	—	C	*		*?				*					*	2	
Mus (House mice)	1	L	—	C	*						*					*	2	
Glis (Dormice)	1	L	—	—	*						*				*	*	4	Koenig, 1960
Zapodidae (Jumping mice)	1	VL	—	X	*						*					*	4	
Jaculus (Jerboa)	1	VL	—	X	(*)							*	*			*	3	Kirmiz, 1962; Happold, 1967; Rosevear, 1969
Erethizon (Porcupine)	4	M	—	C	*					?						*	4	
Dasyprocta (Acouchi)	3	S	4	C	*						*						4	Morris, 1962
Lagidium (Mountain viscachas (chinchillid))	3	L	—	—	*						*						2	Pearson, 1948
Canis domesticus (Dogs)	2,3,4,5	M,L	1	B,C,D	*			*	*	*							—	Hildebrand, 1967
Wild canids	3,4,5	M,L	1	A,B,C	*			*		*						(*)	2	
Ursus arctos (Brown bear)	6	S	3	B	*					*						*	4	
Ursus maritimus (Polar bear)	6	S	3	B	*				*?	*						*	1,6	Harington, 1970
Ursus americanus (Black bear)	5	S	3	B	*		*?			*					*	*	4	Van Wormer, 1966; Whitney & Underwood, 1952
Procyon lotor (Raccoon)	4	M	1	C	*		*	*		*					*	*	4	Rue, 1964
Mustela (Weasels, Mink)	1,2	M	4	D	*			no			*				*	*	4	
Lutra (Otters)	4	L	4	D,E	*		*	no		*	*					*	1	Tarasoff *et al.*, 1972; Park, 1971

Mephitis (Skunk, striped)	3	L	1	C	*				*				*	2	Verts, 1967
Gulo (Wolverine)	5	L	1	C	*		*		*			*	*	4	
Martes (Marten, Fisher)	2,3	L	4	D	*		no		*			*	*	4	
Enhydra (Sea otter)	5	M	4	E	*					*				1	Tarasoff *et al.*, 1972
Meles (Badger, European)	4	S	1	C	*		*		*			*		4	Neal, 1948
Tayra (Tayra)	3	L	1	B	*		*		*			*		2	
Mellivora (Ratel)	4	S	1	B	*		*		?			*		4	Lawick-Goodall, 1970
Ichneumia albicauda (White-tailed mongoose)	3	L	1	C	*		*			?		no		2	Taylor, 1970
Mungos mungo (Banded mongoose)	2	L	1	C	•		*			*		no		2	Taylor, 1970
Helogale parvula (Pygmy mongoose)	2	L	1	D	•		*			*		no		2	Taylor, 1970
Suricata suricatta (Grey meerkat)	2	L	1	C	*		no		*				*	6	Ewer, 1963
Nandinia binotata (Palm civet)	2	L	1	D	*				*					4	Dücker, 1971
Hyaena hyaena (Striped hyaena)	5	L	2	A	*		?		*					6	
Crocuta (Spotted hyaena)	5	M	2	A	*		no		*			no		6	Kruuk, 1972
Felidae (All cat family)	3,4,5	S,M,L	1	B,C	*		*		*	*		*		2	
Elephantidae (Elephants)	7	M	1	A	*	•								4	Matthiessen, 1972
Equus caballus (Horse)	6	M	1	B	*	*	*	*	*					6	
Other equids	5,6	M	1	B	*		*		*					6	
Tapirus (Tapirs)	6	S	1	B,C	*		*		*					4	R. & S. Wilson, personal communication
Rhinocerotidae (Rhinoceroses)	7	M	1	C	*		*		*					4	
Suidae (Pig family)	5	L,M	1	B,C	•		*		*					4	
Tayassuidae (Peccaries)	4	S	1	A	*		*		*					6	
Hippopotamus (Hippopotamus)	7	S	1	C	*		*		no					1	
Camelus dromedarius (Dromedary)	6	M	1	A	*			*	*					3	Dagg, 1973
Lama (Llama)	5	S	1	A	*			*	*					6	Personal film
Vicugna (Vicugna)	5	S	1	A	*		no		*					6	Koford, 1957
Cervidae (Deer)	5,6	S	1	A,B	*		*		*		(*)			4	Dagg & de Vos, 1968a, b
Camelopardalis (Giraffe)	7	M	2	A	*		no		*		no			4	Dagg & de Vos, 1968a, b
Okapia (Okapi)	6	M	1	A	*		no?		*		no			4	Dagg & de Vos, 1968a, b
Antilocapra (Pronghorn)	5	S	1	A	*		*		*		*			6	Dagg & de Vos, 1968a, b
Bovidae (Bovids)	3,4,5,6,7	S,M,L	1,2,3	A,B,C	*		*		*		(*)	(*)	(*)	2	Dagg & de Vos, 1968a, b

	Formula	
A	over 11	long legs
B	9–11	
C	7–9	
D	5–7	
E	under 5	short legs
X	hind legs especially well-developed	

In addition to collecting gait information from the literature, films were taken in the laboratory of various small mammals, although useful information was difficult to obtain because the animals moved so irregularly. Some data were also taken from tracks (Murie, 1954). The type of track was easy to identify if the animal was bounding or galloping, but not if it was walking, trotting or doing the running walk.

(5) Habitat (Column 17)

The habitat preferences of the animals were divided into the following categories:

1 Near water
2 Varied
3 Arid
4 Woodland
5 Arboreal
6 Savannah or tundra

(6) References (Column 18)

References were only given for those mammals whose gaits had been studied in detail in a particular paper.

DEFINITION OF GAITS

Zoologists often neglect to define the gaits of mammals they specialize in, possibly because they do not understand them. They should realize that the quadrupedal gaits for example are distinct and used for different speeds, and that they do not intergrade with each other to any extent; the walk for example could be considered as first gear of a car, the trot or pace as second gear and the gallop as third gear. For any animal travelling at a given speed there is an optimal gait which minimizes the total work done (Smith & Savage, 1956). To elucidate the gaits, they are illustrated in Fig. 1 and defined as follows.

Walk (Column 5 in Table 1). The slowest gait, in which two, three or four legs support the body at any one time. It is symmetrical, with the left legs repeating the movements of the right legs, half a stride later. It can be subdivided into various components (Hildebrand, 1966).

Walk using tail (Column 6). The slow symmetrical gait of some species which have enlarged hind legs, in which the tail forms an important supporting member.

Running walk (Column 7). A quick walk sometimes called an *amble*, with the footfalls the same as those in the walk. At least one hind and one front leg usually support the animal. This gait cannot be sustained for long periods.

Trot (Column 8). The symmetrical gait of intermediate speed in which two diagonal legs usually support the body when it is in contact with the ground. It is not synonymous with the slower 'walking trot' defined by Hildebrand (1967).

Pace (Column 9). The symmetrical gait of intermediate speed in which two lateral legs usually support the body when it is in contact with the ground. *Pace*, not *rack*, is the accepted word for this gait in harness racing of horses around the world.

Gallop (Column 10). The fastest gait, in which the body is often unsupported following a push-off with the hind legs and sometimes with the forelegs. It is asymmetrical, with the right and left legs doing different movements in a stride. This gait includes the canter and the lope. These movements may intergrade with those of the bound in many species.

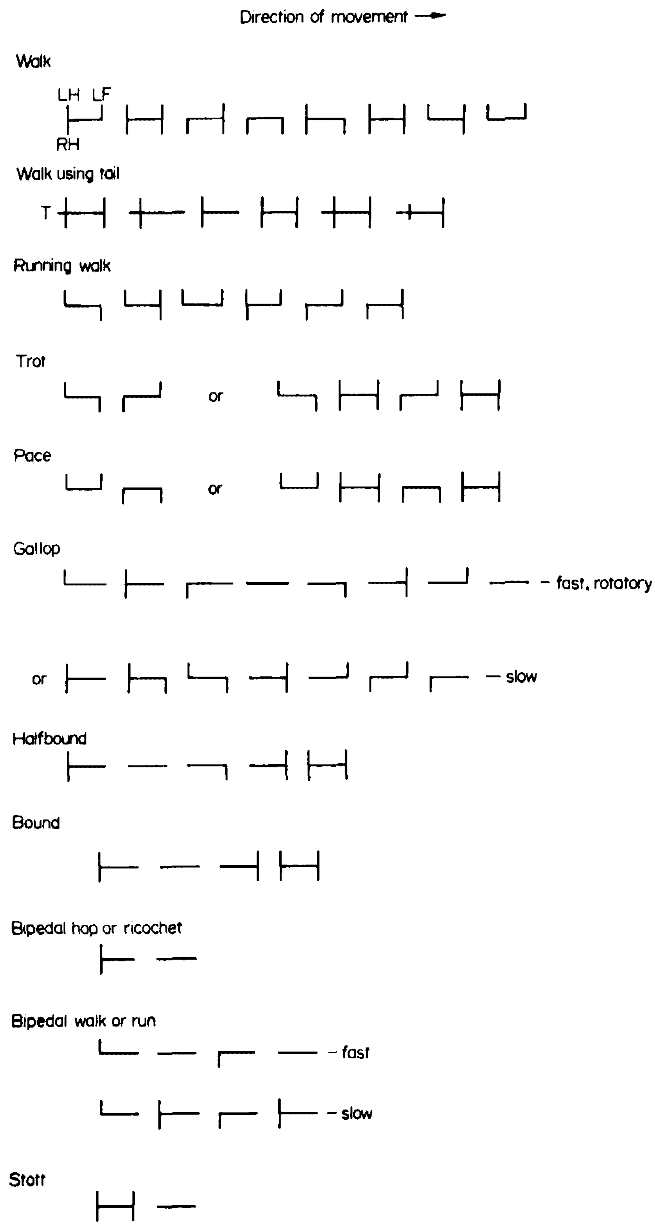

Fig. 1. Typical sequences of combinations of supporting legs in strides of mammalian gaits. L–left; R–right; F–front; H–hind; T–tail.

Bound (Column 11). A fast gait in which the front legs and back legs move together in pairs. The *half-bound* is included in this category; the push-off is always from the hind feet but in the bound the animal lands on both forefeet together. Since this cuts down the velocity of forward motion considerably, many animals put one front leg down and then the other, which is the half-bound.

Bipedal hop or ricochet (Column 12). The animal travels only on its hind legs, either slowly or quickly, moving the hind legs synchronously.

Bipedal walk or run (Column 13). The upright animal moves either slowly or quickly, but using only the hind legs and these alternately.

Stott (Column 14). This gait, also called the pronk or the spronk, is performed with all four legs taking off and landing together. During the period of suspension the legs hang down vertically from the body.

Display gaits (not designated). These serve not only to transport an animal from one place to another, but to communicate the emotions of the animal to others. They do not include non-continuous movements like the stamping of feet to warn of danger.

Prost (1970) feels that these classic gaits will become obsolete in a scientific description when more exact analyses have been made of various quadrupeds. Such analysis will not likely come about for many years, but in any case the terms described above will still be in general use.

Two other categories related to movements are given in Table 1.

Climb (Column 15) refers to the animals' ability or lack of it to climb trees.

Stand (Column 16) refers to their ability to balance erect for significant amounts of time on their hind legs.

DISCUSSION OF GAITS

Quadrupedal walk

This slow gait is present in most quadrupedal mammals with the exception of some that have their hind legs much more developed than their forelegs and of some that are entirely arboreal. Except for a few primates, mammals with unusually large hind legs nearly always move these legs simultaneously and not alternately, either by themselves or in conjunction with the front legs, a condition not true for reptiles (Snyder, 1962). Such mammals include kangaroos, wallabies, small jumping rodents, Spring hares and chinchillids. Although ancestral animals in the basic kangaroo stem evolved as hopping terrestrial forms, the Tree kangaroos subsequently moved into trees where a hopping gait is not suitable. These animals unlike other macropodins sometimes use a quadrupedal walk along branches or ledges in zoos (Windsor & Dagg, 1971). Similarly, whereas most lagomorphs hop or bound, some occasionally walk. This is a not uncommon gait in rabbits that must manœuvre on mud, such as the Swamp rabbit *Sylvilagus aquaticus* and the Marsh rabbit *S. palustris* (Terrel, 1972; Tomkins, 1935); a soft substratum is a poor one for a hopping gait which necessitates a large downward thrust on a small area. Lagomorphs that can walk but rarely do so include the Blacktail jackrabbit (Murie, 1954), the Whitetail jackrabbit and the Varying hare (Jackson, 1961) and the cottontail (personal films). Walking is less foreign to lagomorphs apparently than to species of chinchillids; newly-born hares walk first before hopping, and swimming rabbits often paddle with alternate legs, something the chinchilla does not do (Nice, Nice & Ewers, 1956; Dagg & Windsor, 1972). It would seem that the simultaneous use of limbs is more deeply ingrained in the chinchilla, possibly because this pattern developed earlier in its evolutionary history.

The arboreal group of mammals that do not use a quadrupedal walk include the sloths, gibbons and orang utan. Since these species seldom move any distance on the ground, they possess no other terrestrial gaits either.

Quadrupedal walk using the tail

Dipodomys and macropodids that use this slow gait all have well-developed tails upon which the animal puts weight as if the tail was a fifth appendage. They swing their hind legs forward while their weight is supported on their front legs and tail (Windsor & Dagg, 1971). Pangolins moving slowly also may use this ponderous gait (Vincent, 1964).

Running walk

This gait may be common in small species, but it can only be identified accurately in them in slow-motion films, so little is known about it. It is an artificial or taught gait in horses and the sole fast gait of elephants. Because of their mass, elephants are usually supported by at least one front and one hind leg. They are unable to trot, gallop or jump so they have been safely confined behind a ditch only 1·7 m wide and 1·4 m deep (Grzimek, 1970).

Trot

This gait is an enduring one of medium speed. To perform it, animals must have front and hind legs of similar length. Thus, it is not found in any of the species with extra well-developed hind legs mentioned in the section on the quadrupedal walk. Nor is it present in some species with sloped backs such as the Ring-tailed lemur, Spotted hyaena, bears (?) and giraffe. It is found in other slope-backed animals however such as the wildebeest and hartebeest and in viverrids in which the front legs are shorter than the back. The back must be fairly straight, as the propulsive force comes from the right hindquarters and left forequarters (or vice versa) at one time. Animals like bears, acouchis, apes and monkeys which do not trot may not have a spine that is straight and rigid enough; in apes the back and pelvis may rotate sharply from side to side during the symmetrical walk, in order to increase the length of stride of the relatively short hind legs (Hildebrand, 1967). Nor can the body be too long as it is in most sciurids and small mustelids; mustelids that are not too long to trot (shape C or B) are the wolverine, European badger, ratel and tayra. Very small animals like Field mice (North American *Microtus* species) can apparently trot, judging from my films, although Harrison Matthews (1969: 83) states that small mammals cannot trot, but only use a fast walk, bound or gallop. Large animals like the rhinoceros and the hippopotamus can trot, whereas the huge elephants cannot.

The pace

As in the trot, animals that pace must have front and hind legs of roughly the same size. Animals with sloping backs like giraffe and hyaenas, and that move their lateral legs almost together in the walk, still do not pace. The animals that do pace are the dog, horse, bears and camelids. Since this rare gait is present in the two domestic animals that have been bred most intensively by man for centuries, it may be that the pacing gait is inherited in many species but that it is useful only in mammals with suitable anatomy or in those that inhabit flat terrain like camels, since the pace is a less stable gait of intermediate speed than is the trot. In horses the use of the pace is governed by a single gene which is recessive to the dominant gene which governs the trotting gait (Kormondy, 1964). Thus, in horses natural pacers are homozygous recessives that breed true. However, trotting horses can be taught to pace with the use of special shoes and hobbles. Among dogs, only long-legged breeds pace. These include the bloodhound, German shepherd, Golden retriever, collie, Great Dane, Rhodesian ridgeback, saluki and weimaraner (Hildebrand, 1968).

Because of its instability, the pace is only useful on flat ground. It has probably developed in the camel (*Camelus dromedarius*) because of this species' flat desert habitat (Dagg, 1973). It has also been filmed in the llama briefly, but the pace is not present in the vicugna (Koford, 1957) which is smaller and may occupy more rocky habitats in the Andes Mountains. A suitable anatomy for the pace, in which the body is supported alternately by the two left legs and then the two right legs, is

(a) a fairly large size, so the mammals will not roll too far sideways while supported by lateral legs (large dogs are minimum in size),

(b) a slim build so that the centre of gravity of the animal can more or less be shifted over these supporting legs (camels, horses and dogs), or

(c) heavy limbs to provide a sturdy support and a low centre of gravity (bears).

The pace and the trot are equally fast in the horse, but the pace is a superior gait in that the front and hind legs never hit each other as may happen in the trot.

Gallop and bound

These are fast gaits which are almost universal in terrestrial mammals since they are used to catch prey or to escape from predators. They are considered together since they are closely allied, although the bound is considered to be a symmetrical and the gallop an asymmetrical gait. For example cheetahs tend to gallop when travelling slowly and to bound when chasing prey; galloping antelope may give occasional high bounds as they flee, to see better or to confuse their predators; and the gait of a marsupial mouse is described as a 'bounding gallop' (Ewer, 1968). Species which only bound and do not gallop have flexible backbones, such as small sciurids, Jumping mice, lagomorphs and long mustelids. Seton (1953) claimed that the tree climbing species in general tend to bound, but this may only be because arboreal mammals are usually light. Species which only gallop and do not bound tend not to have long bodies and to have quite rigid backbones, such as ungulates, canids, ursids, hyaenas, large sciurids like the woodchuck and large mustelids like the skunk and the wolverine. Perhaps because of an inflexible backbone and a low-slung body some primitive quadrupeds like the opossum and the platypus are unable to gallop or bound.

As for the trot and pace, mammals that gallop must have front and hind legs of similar size, although the differences in length may be greater. In the macropodids most kangaroos and wallabies do not bound but the Tree kangaroos and quokkas do. These species have relatively longer forelegs than do confamilial mammals.

Some mammals are so heavy that they cannot hoist themselves into the air for a gallop. Thus, elephants (max. 7000 kg) and hippos (max. 3000 kg) do not gallop but rhinos (max. 2000 kg) do. (Similarly Malaysian crocodiles less than 2 m long can gallop, whereas larger ones never do (G. Zug, personal communication)). Even when hippos are moving underwater where they are buoyed up by the water, they trot rather than gallop, inferring that a gait which had never been learned would not suddenly be used.

Many mammals can both gallop and trot, but they habitually use one gait rather than the other to cover distance quickly. Large animals such as the moose, elk, caribou, eland and waterbuck tend to trot rather than gallop at speed (Dagg & de Vos, 1968b). The trot may be preferred for any of the following reasons:

(a) The trot is less tiring, although the gallop is faster. (Park (1971) claims that otters glide *because* this provides a rest between galloping sequences.)

(b) The trot is more stable, since two diagonal legs support the animal for most of each stride. One leg rarely supports an animal by itself as it does often in the gallop. Thus the trot is a better gait on mud or snow substrate or along a rough trail in thick vegetation.

(c) The centre of gravity changes less drastically during the trot than it does during the gallop. Large animals, especially those with heavy horns or antlers, would find a gallop particularly tiring, since these would have to be lifted higher during each stride in the gallop than in the trot.

Bipedal hop or ricochet

The animals which habitually hop using only their hind legs have enlarged hind legs and long and heavy or tufted tails which are held aloft at speed as a counterbalance. They can either be large, like kangaroos or small, like Kangaroo mice. Ricochetal terrestrial mammals are always primary consumers and usually from desert areas.

Although they cannot be called ricochetal mammals, there are two other groups that hop on their hind legs on occasion. The first group includes some lagomorphs, especially the Arctic hare and the Greenland hare (Tener, 1954; Seton, 1953). These species use it when they are closely pursued. They can climb hills and zig-zag readily while using it, but its advantage over the bound is so far unknown. Perhaps the short tails of hares prevent a ricochet from becoming a major part of their locomotion. Leaps on the hind legs are used occasionally in a series of successive spy-hops by Whitetail jackrabbits escaping in long grass (Cahalane, 1947).

The second group includes various long-legged prosimians which leap from tree to tree in their arboreal habitat, but also which ricochet occasionally on the ground. They include species of *Indri*, *Propithecus*, *Avahi*, *Galago*, *Tarsius* and perhaps *Lepilemur* (Lessertisseur & Petit-Maire, 1972).

Bipedal walk or run

In this gait the animal travels on the hind legs only, moving them alternately. This gait was used by some extinct reptiles probably, and is used by some modern lightly-built ones. The two groups of mammals that use it are some primates and a few species with well-developed tails, including pangolins, Kangaroo rats and jerboas. The latter always move slowly in this gait, with their tails dragging along behind them.

A more active bipedal walk or run is present in long-legged prosimians, monkeys and apes. Capuchin and Spider monkeys run bipedally, the latter with its trunk leaning forward and its tail held out backwards for balance, or with its arms raised above its head and its tail also raised vertically, since the centre of gravity then runs down through the body.

Stott

The stott is confined to gregarious pecoran species (Table 2). Although it is slower than a gallop, it is effective in changing direction and in climbing hills. It presumably acts in intraspecific communication, (a) by allowing the pronking animal to be seen by others, particularly if it has a distinctive rump or tail as it usually does, (b) by making a distinctive noise which may warn of danger, and (c) by often depositing scent on the ground from interdigital or pedal glands. It also gives the fleeing animal a good view from the height of the bound. Since the hooves are set down close together, this gait may help prevent them from becoming entangled in dense vegetation and offer the animal a rapid start.

Table 2

List of mammals that use the stott

Elk	*Cervus canadensis*	Struhsaker, 1967
Mule deer	*Odocoileus hemionus*	Dagg & de Vos, 1968b
Fallow deer	*Dama dama*	Matthews, 1969
Pronghorn	*Antilocapra americana*	Dagg & de Vos, 1968b
Blackbuck	*Antilope cervicapra*	Schaller, 1967
Nilgai	*Boselaphus tragocamelus*	Schaller, 1967
Thomson's gazelle	*Gazella thomsoni*	Estes, 1967
Grant's gazelle	*Gazella granti*	Estes, 1967
Oribi	*Ourebia ourebi*	Struhsaker, 1967
Impala	*Aepyceros melampus*	Lent, 1966
Springbok	*Antidorcas marsupialis*	Matthews, 1969
Saiga	*Saiga tatarica*	Murie, 1870
Lechwe	*Kobus leche*	Dagg & de Vos, 1968b
Reedbuck	*Redunca arundinum*	Dagg & de Vos, 1968b
Kongoni	*Alcelaphus buselaphus*	Estes & Goddard, 1967
Wildebeest	*Connochaetes taurinus*	Kruuk, 1972

Display gaits

Display gaits, which reveal information about the behaviour of individuals, are used often in gregarious species. Among primates, a dominant male often strides along with a 'slow and deliberate' walk (Stump-tailed macaque), a 'swaggering walk' (Ring-tailed lemur), a 'confident gait' (Olive baboon), a 'confident walk' (Vervet monkeys) and a 'strutting walk' (gorillas), all quoted in Bertrand (1969).

Observations have also been centred on gregarious ungulates which live on open plains where they can see each other and be seen by zoologists. The most common behavioural gait is perhaps the *prance*, in which a breeding or territorial animal, usually a male, moves with a stiff-legged gait using short, accentuated steps. Schaller (1967) observed breeding males with head held high prancing near oestrous females in chitals *Axis axis*, Hog deer *Axis procinus* and Swamp deer *Cervus duvauceli*. Prancing is also present in blackbuck, Grant's gazelle, oryx (Buechner & Schloeth, 1965) and kob (Bere, 1966).

Other behavioural gaits include the *warning gait*, in which a disturbed animal walks with stiff high steps, sometimes preparatory to charging. Altmann documented this in elk (*Cervus canadensis*) and moose (*Alces alces*) (Altmann, 1958). Often subordinate individuals move with small fast steps while dominant ones use large swaying steps.

In the Barren ground caribou, Lent (1966) found that neonate calves could be aged by their gaits, since the hind legs do not straighten entirely until the third day of life. A female with calf also exhibited an unusual running gait, with much vertical movement, if her calf was in danger. During this gait, which told hunters her calf was nearby, the female held her head high and her rostrum parallel to the ground.

Small mammals probably also have display gaits, but few have been documented. Poole (1967) has however defined an 'arch-back trot' for ferrets which is used when one female encounters another.

Too few display gaits have been described so far to make a comparison of them worthwhile. In the future though, when more of them have been documented, this should be an interesting field of study, particularly from an evolutionary point of view.

Climb

The ability to climb is not always correlated with suitable anatomical adaptations. Many species are obviously adapted for arboreal life (such as prosimians, most monkeys, most apes, sloths, squirrels, many marsupials), but some arboreal species are very similar to their terrestrial relatives (Tree kangaroos, Tree hyrax, fisher and marten). A tail is most useful to many arboreal mammals, such as New World monkeys; species of *Peromyscus* that inhabit trees have longer tails than do terrestrial species (Horner, 1954). But a tail is small or lacking in others such as gibbons, sloths and Tree hyrax. No climbing species are excessively large, since trees would not support them; probably small bears, male gorillas and lions reach the maximum size of mammals that climb trees. Usually such arboreal animals have flexible limbs to enable them to grasp branches, but goats climb into trees in arid regions of Morocco to browse (Harrison Matthews, 1969) and Gray foxes are sometimes seen in trees (Yeager, 1938; Terres, 1939).

Stand

The ability to balance on the hind legs, usually to see better, is common in small mammals and universal in ricochetal ones. It is even present in bears, which have short well-muscled legs and hindquarters on which to balance. It is uncommon in cursorial prey and predator species which have long, thin legs.

FACTORS AFFECTING GAIT

Morphology

The morphology of an animal determines its gait to a great extent. Harrison Matthews (1969) described an Alsatian dog which had lost two ipselateral legs; it was able to bound but not to walk. Similarly a goat born without forelegs was only able to hop. The parameters that limit the possible gaits of a species are apparently:

(1) *Weight*

Graviportal mammals are limited in their gaits and speed. The fastest gait of the elephant (up to 7000 kg) is the running walk, to 24·5 mph (Howell, 1944) while that of the hippo (up to 3000 kg) is the trot, to about 20 mph. Rhinoceroses (up to 2000 kg) can also gallop, at speeds up to 35 mph (J. G. Goddard, personal communication). All the gaits are possible for the small mammals.

(2) *Slope of back*

(a) *Back more or less flat.* These mammals usually have the common quadrupedal gaits, but lack the bipedal ones.

(b) *Back sloping up to head.* A sloping back may or may not affect a species' gaits. The giraffe, Spotted hyaena, gorilla, chimpanzee and baboon lack a trot or a pace, but the wildebeest and the hartebeest can trot like other bovids. The differences may be reflected in the steepness of the slope or in other facets of the morphology.

(c) *Back sloping down to head.* Mammals whose back slopes down to the head include bears, some viverrids, the Ring-tailed lemur and some forest bovids like the bongo. Such a shape may make the Polar bear more stream-lined in water and the other species better able to manœuvre through dense vegetation. The slope of the back, which is never great, does not affect the gaits of these mammals significantly.

(*d*) *Back distinctly humped.* The humped shape of many mustelids is apparently correlated with their elongated trunks, which are suitable for swimming or for squeezing through small openings. These mustelids do not trot. The pangolins and armadilloes have humped backs because of their curved 'armour', in which they roll up if attacked.

(3) *Body shape*

The very long Sea otter and River otter of shape E do not trot but some mammals of shape D do, including the Pygmy mongoose, bloodhound, Field mouse (*Microtus*), hedgehog and opossum. Some mustelids, some sciurids and the platypus (all shape D) do not trot. The platypus may not do so because it is too cumbersome and unable to raise its body directly over its legs.

The long legged mammals of shape A and B tend to be the highly evolved cursorial prey and predator species plus many monkeys and apes. The cursorial species usually possess the common gaits but they are able to execute them with extra speed because of their long legs and therefore long strides. Long legs make primates particularly agile in trees, but do not enable them to trot or pace.

(4) *Elongated hind legs and bipedalism*

Extensive bipedalism has evolved in three orders of mammals—in marsupials, in rodents and in primates. Many primates move on two legs so that they can fight effectively or carry food or an infant and most can stand erect briefly to see well. Some primates such as sifakas and Spider monkeys use their long tails on the ground to help them balance while standing upright, like tripods. Primates in trees spend large parts of each day with their trunks in an upright position while sitting or while brachiating, as gibbons, Spider monkeys and Woolly monkeys do. From such an upright posture bipedalism in primates perhaps evolved because of the need for the anterior limbs in climbing in trees. A ricochetal leap is important for an animal that is leaping from one tree or branch to another. The strong hind legs push off together and the front legs grasp the terminal tree. Alternate leg movements are important when climbing about in a single tree. Lessertisseur & Petit-Maire (1972) underline, however, that the bipedalism of man is not derived either from a leaping prosimian stock nor from a brachiating stock. A terrestrial bipedal gait in non-human primates is often not a stable one. For example the Stump-tailed macaque can run but not walk on two legs (Bertrand, 1969); the slow gait requires more balance than the macaque can apparently master.

Extensive bipedalism that evolved in terrestrial mammals other than man is always ricochetal, with the hind legs moving together. Hatt (1932) postulated that the bipedal ricochet in rodents was correlated with the strengthening of the hind limbs which allowed a steeper trajectory during jumps. Some mammals like Jumping mice and Pocket mice jump quadrupedally in grassy areas, although they usually 'freeze' if in danger, while hopping animals in deserts tend to hop bipedally. Bartholomew & Cary (1954) suggested that the evolution of bipedalism in heteromyids was basically a by-product of specialized foraging habits and that the advantage gained by ricocheting in escaping from predators was of secondary significance. It must be important however or it would not have evolved in various different evolutionary lines. Snyder (1967) argued that sudden directional changes are useful in the desert where there is little vegetation to hide in and are easier for bipedal mammals that use their legs together rather than alternately. In ricochetal forms a greater proportion of the propulsive power is involved in the upward thrust, and available limb power at each point of contact with the ground is twice that of an animal that uses its legs alternately. However, an alternate bipedal gait, which is faster than a ricochetal one and requires less energy, has been adopted by some small desert lizards which also have a quick-starting, evasive form of locomotion. The fact that the ricochet has evolved more often than an alternate bipedal gait may be correlated with the lack of broad-based feet on which to balance the entire length and weight of a moving body, however momentarily (Snyder, 1967).

Kangaroos are the only large animals with an exclusively ricochetal fast gait. With it they can travel up to 40 mph (Grzimek (1967) gives a speed of 55 mph). Whether it would have been retained if there had been more effective predators present during the evolutionary history of the kangaroos must remain unknown.

(5) *Tails*

The tail affects a species' gaits in a variety of ways. The long tail of a cursorial animal like a dog or a cheetah helps it change direction while running, but the tail may also be useful during slow gaits; in the walking opossum the tail moves both laterally and vertically, describing a figure eight (McManus, 1970). The tail is particularly useful for some climbing species such as monkeys, opossums, porcupines and rats, in which it is pressed against or wrapped around tree branches. Among the Tree shrews, those tupaiids with tails shorter than their bodies generally are terrestrial whereas those with tails appreciably longer than the body are arboreal. *Tupaia belangeri*, which is semi-arboreal, has a tail length similar to that of its body length (Martin, 1968).

The tail is long in all saltatorial species both large and small. For example the long tail of the Kangaroo rat *Dipodomys* acts both passively and actively as a balancer during hops and is used as a prop when the animal stands erect. When the tail of one individual was cut off, it turned a complete forward somersault during an attempted high leap (Bartholomew & Caswell, 1951).

However, there are many factors besides gait that may have affected the morphology of the tail during its evolution. For example, the tail of mice has been shown to be an important thermoregulatory organ (Harrison, 1958), as is the tail of the fox; that of *Ctenomys talarum* is used as a sensory device in backing quickly into its tunnel (Weir, 1971); those of ungulates are important as fly switches; tails are often essential in intraspecific communication; and that of *Peromyscus floridanus* is easily broken and thus serves as an escape mechanism (Layne, 1972).

Phylogeny

From a study of only the morphology of various species one could easily assume they had gaits which they in fact do not have. Superficially one would imagine, although it is not so, that vicugnas, camels and okapis should trot because bovids of similar shapes do, and that pikas should walk, not hop, because their front legs are similar in length to their hind legs.

It is reasonable to theorize, because of these anomalies, that phylogeny is also important in determining the gaits of mammals. Given this hypothesis, it would seem that gaits that are deeply embedded in a group of mammals, or in other words gaits that are used to a great extent by them, are gaits that appeared early in their phylogenetic line. Thus one can infer the phylogeny of a group by considering the gaits of the extant species. This has already been demonstrated for the kangaroo family (Windsor & Dagg, 1971). The quokka and the Tree kangaroos that bound as well as ricochet are thus believed to be relatively primitive species, while *Wallabia bicolor*, which has a distinctive mode of slow progression, is thought to be monotypic and not closely related to the other species of *Wallabia* because of this.

As another example, since the hopping pattern of movement is more deeply embedded in the chinchillids (used even by swimming individuals) than in the lagomorphs (which often swim with alternate legs), apparently a hopping gait evolved earlier in the phylogenetic tree of the chinchillids. We could assume that a chinchillid ancestor would be more likely to hop than would a lagomorph ancestor living at the same time.

A further example relates to the movement of the right and left legs, which may move together or separately. The use of one method alone, as the trot in felids or the pace in camels, indicates that a single pattern is of older significance in their phylogeny than it is in the phylogeny of the horse or dog which can both pace and trot.

As well as considering the phylogeny of gaits from a vertical or historical point of view, one can take a horizontal approach by considering the ontogeny of gaits in living mammals. Based on the premise that in some respects ontogeny does recapitulate phylogeny, we can infer that the ability to move the right and left legs alternately is basic to all tetrapods. Even animals that move their legs synchronously as adults, such as lagomorphs, macropodids and bipedal rodents, have neonates that move their legs alternately (as Grange, 1932; Reynolds, 1958; Chew & Butterworth, 1959; McManus, 1971). For example in the case of the adult rabbit, which rarely or never walks, Ten Cate (1964) has shown experimentally that there are nervous mechanisms both for synchronous jumping movements and for alternate walking movements in the hind limbs of rabbits.

Just because some mammals are cursorial does not mean that they are evolving in such a way that their speed is maximized. Mech (1966) has made relevant observations on moose. On Isle Royale in Lake Superior where wolves killed a moose about every 3 days, the moose that ran from these predators were more likely to be killed by them than were those that did not. Thus, natural selection was not working here to produce moose with gaits of increasing speed.

An example relating to this efficiency of gaits is given by Taylor (1971) for viverrids. He found that in his study of 308 dead individuals, 15% of them had some skeletal pathology because of earlier fractures or disease which would certainly have affected the gaits of most of them. Thus, these non-cursorial mammals had been able to find food and survive, even though they had difficulty moving naturally.

Habitat

The environment of mammals has played a notable part in influencing their gaits. The best examples are the deserts of the world where hopping marsupials and rodents are characteristic, although even here one cannot asseverate that the ricochet is best for small mammals. Marlow (1969) has discussed two small mammals *Notomys* and *Antechinomys*, both from the same Australian deserts and both with elongated hind legs; yet the former hops bipedally at fast speeds and the latter hops quadrupedally. The desert also is responsible for the presence of the rare pace in camels (Dagg, 1973).

In savannah lands there are many bounding species like lagomorphs, Spring hares and Jumping mice, but species with many other gaits as well. The walks of cursorial mammals from savannahs tend to have long periods of support by lateral legs, compared to the walks of woodland pecoran species (Dagg & de Vos, 1968a). Forest habitats not only affect the walks of woodland species, making them particularly stable and capable of quick retreat in event of danger, but they affect the gaits of arboreal species such as sloths, primates and Tree kangaroos.

Some groups have species adapted to several habitats. Thus, tundra lagomorphs ricochet as well as bound, boreal lagomorphs only bound, and Swamp and Marsh rabbits walk as well as bound. However, the gaits of mammals often cannot be related so directly to their present habitat. Undoubtedly the past habitat too can be assumed to have influenced the evolution of mammals immensely and thus their gaits as well.

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