



Gaits and energetics in terrestrial legged locomotion

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Abstract

In spite of the sustained worldwide efforts of the last few decades, the development of mobile robots with legs is mostly restricted to laboratories. The performances of these machines are far inferior to those of legged animals. In this paper, we study the observations made by various researchers on animal locomotion. This is done with the hope that engineers trying to design and develop legged robots would find such information useful. We focus our attention on the gaits of animals and the energy they consume for locomotion.

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1. Introduction

Man made means of terrestrial locomotion are based mainly on the wheel, while mammals and insects use mainly legs for locomotion. Wheeled vehicles need prepared surfaces. Almost half of earth's land surface is inaccessible to them. Legged animals can move over most of earth's terrain, and in principle, legged machines should also be able to. Our dependence on transportation based on wheeled locomotion is a major source of damage to the natural environment. On the other hand, legs create discrete footprints and cause less damage to natural terrain. In addition, comfort of transportation or isolation from terrain irregularities also favors legged locomotion. These facts indicate the importance of legged machines. With the advances in control of complex systems, efforts to develop legged machines have become more intense.

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Animals tend to evolve the best possible structures and behaviors. The purpose of this study is to get an insight into various mechanisms evolved in biological systems to make legged locomotion diverse and efficient. Features responsible for effective legged locomotion in *biological machines* could provide directions for designing and building machines that can walk on legs, maintain stability on uneven terrain, move faster and consume less energy.

In the next section, the basic concepts of animal gaits are discussed, and gaits of hexapods, quadrupeds and bipeds presented. Section three deals with energetics of legged locomotion. Effect of gait, speed, weight and limb posture on energy expenditure are discussed here.

2. Gaits of terrestrial legged animals

A leg is not a continuous locomotion element like a wheel. Therefore, it must be lifted at the end of its effective stroke, returned and placed on the ground to begin another support phase. A gait of an articulated animal is the *corporate motion of the legs*; coordinated with the motion of the body in order to move it from one place to another in such a manner that stability is always maintained. A gait can be statically or dynamically stable. The basic requirement to achieve static stability is that the projection of animal's mass center should pass through the region covered by feet on the ground. In dynamically stable gaits there is no such constraint. Quadrupeds at high speed and bipeds rely on dynamic stability. The gaits that animals select depend on factors like body proportions, speed and agility, energy expenditure, neuromuscular control that is required, etc. Study of gaits helps to understand the physiological basis of gait selection and also helps to establish the limits of performance.

In 1887, Muybridge triggered a battery of still cameras to take sequential photographs of moving animals and published [1] the first accurate depictions of various gaits of horses and other animals. Muybridge used *support sequences* to indicate the sequence of combinations of supporting feet in each locomotion cycle (Fig. 1a). Black circles indicate that corresponding legs are in the support phase (on the ground) and the arrows indicate the direction of motion of the body during the corresponding foot patterns. However, support sequence does not show the relative durations of various phases of support. Gaits differing somewhat in timing can have the same sequence. In 1965, Hildebrand [2], developed the concept of gait formula to describe gaits by introducing *gait diagram*, which plots support by each foot against a time scale (Fig. 1b). The

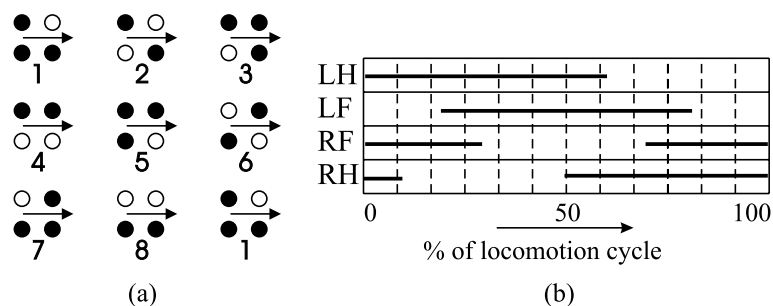


Fig. 1. Gait representation.

beginning and end of a darkened line correspond respectively to the placing and lifting of corresponding foot. However, for comparison and classification of many such diagrams it is necessary to convert gait diagram to numerical expression without sacrificing any information. In 1968, McGhee [3] extended the work of Hildebrand and contributed a strong mathematical base. Some of the important terms used with regard to gaits are given here.

Protraction is the forward movement of a leg relative to the body and ground. *Retraction* is the backward movement of a leg relative to the body with no movement of the leg relative to the ground. The *transfer* phase (or swing) of a leg is the period in which the leg is not on the ground. The *support* (or stance) of a leg is the period in which the leg is on the ground. The *cycle time* is the time for a complete cycle of locomotion. The *duty factor* of a leg is the time fraction of cycle time for which that leg is in the support phase. The *leg phase* of a leg is the fraction of cycle time by which the contact of that leg on the ground lags behind the contact of the front leg of left side. The *stride length* is the distance the center of gravity translates during one complete locomotion cycle.

2.1. Gaits of hexapods

The limb movements of many arthropods occur in metachronal sequences (each leg lifts when the leg behind it is on ground), often sequences running from posterior to anterior. Wilson [4] showed that many of the common gaits observed in insects could be generated by changes in just one variable namely the time. In particular, Wilson accounted for the smooth transition between a metachronal gait at low walking speeds and an alternating tripod gait at high speeds. As per Wilson's hypothesis, leg movement in insects follows some general rules. These are:

1. Forward movement of legs relative to the body runs from posterior to anterior and no leg protracts until the one behind is placed in a supporting position.
2. Contra lateral legs of the same body segment alternate in phase.
3. Protraction time is constant.
4. Retraction time decreases as frequency of stepping increases.
5. The intervals between steps of the hind leg and fore leg and between the middle leg and fore leg are constant. However, the interval between the fore leg and the hind leg steps varies inversely with stepping frequency.

According to Wilson, no other patterns, using six legs have been reported for straight walking. Later, he added modifying conditions to accommodate much of the experimental evidences from other animals. However, in special cases, the model is either inaccurate or does not hold at all. For example, climbing grasshopper moves the two legs of a segment together. At slow speeds, mantis is also functionally quadrupedal using only the posterior two pairs of legs.

Delcomyn [5,6] made a detailed study on the cockroach *Periplaneta americana* and found nearly linear relationship between average frequency of leg movement and rate of forward progression. The stride length of the insect is more or less constant. Except at very low speeds (stepping frequency less than 3 Hz), it always uses the alternating tripod gait. At higher speeds, it runs with its body raised well off the ground and its anterior end elevated relative to the posterior. It switches to a gait using only four hind legs. In this posture, the body is propelled primarily by

the long hind legs. Increase in angle of attack of the body also allows greater range of movement through which the hind legs can swing.

Amputation of legs is a popular technique in the study of coordination of leg movements in insects [4,6]. Very often, after amputation, protraction time for the remaining legs becomes smaller in proportion to stepping cycle time. Each leg must bear weight for longer duration. When a front leg is removed, middle legs reach further forward to support the front of the insect. When one leg from each side of the animal is removed, regardless of what combination of four legs remained, the insect adopts the gait typical of a walking tetra pod.

2.2. Gaits of quadrupeds

Among all quadrupeds, the horse is the best documented. Broadly, quadrupedal gaits can be divided into two categories: symmetrical and asymmetrical. In symmetrical gaits, the motion of the feet of any left-right pair is exactly half a cycle out of phase. Interestingly, the quadrupedal animal gaits have specific names. Walk, trot and pace (or rack) are three principal gaits in symmetrical category while gallop is an example of asymmetrical gait. As quadrupedal animals increase speed, they typically switch from walk to trot (or pace), then trot to gallop, with the stride frequency increasing with speed. After reaching gallop, further increase in speed is achieved by increasing stride length while stride frequency remains relatively constant [7].

Walk is the primitive system of locomotion for all terrestrial vertebrates. At slow speeds, animals follow this gait. In normal quadrupedal walk, each pair of legs move in the manner of the bipedal walk but there is a phase difference of quarter of a cycle between the fore and hind legs. Support remains alternatively on two feet and three feet. But, at very low speeds, alternation of three feet and four feet occurs and each foot is placed in regular succession on the ground in advance of its preceding foot being lifted there from. Ox, goat, hog etc. are representatives of double toed or cloven foot animals. On the other hand, elephant, dog, lion etc. are soft footed animals. Support sequences of a walking horse is shown in Fig. 1a. Amble is an accelerated walk and has same sequence of footfall but in more rapid succession. For elephant, walk and amble are the only two gaits in its natural state.

The trot is a system of progress in which each pair of diagonal feet is alternately lifted with more or less synchronism. Two feet do not often strike the ground in exact unison. In Fig. 2a, support sequence of a trotting horse is shown. Here, fore foot strikes just before the hind. When two feet strike the ground in exact unison, the trot is said to be *square* (Fig. 2b). Most mammals use this gait at medium speed. In pace, the legs of same side of the body swing more or less

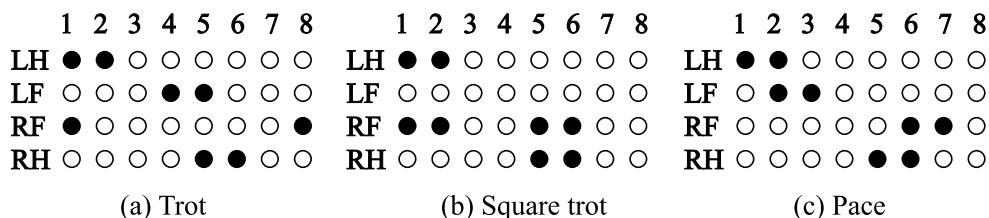


Fig. 2. Stepping sequences in horse.

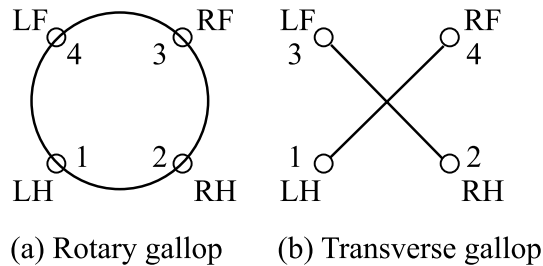


Fig. 3. Gallop in quadrupeds: (a) rotary gallop; (b) transverse gallop (L: left; R: right; F: front; H: hind).

together. Pacers usually place the hind foot down before the fore foot (Fig. 2c). Pace has the disadvantage for short legged animals because stability is reduced. But, the important advantage for long legged animals that a hind foot cannot strike a fore foot. However, not all long legged animals pace but animals those do pace are all long legged. Camel, giraffe use the slow running pace. Both trotters and pacers have the advantage that two legs work together to propel the animal and to cushion the shock.

Gaits in which speed demand is maximum, are the high speed gallops. In this gait, the feet of each pair (fore and hind) are set down almost simultaneously. In rotary gallop, foot impacts individually succeed each other in such a way that these can be orderly placed in the periphery of a circle (Fig. 3a). Foot impacts during transverse gallop can be orderly placed at the ends of a cross (Fig. 3b). If the hind feet strike the ground approximately in unison and the fore feet do likewise, the gait is called bound (or pronk if all feet strike at a time). Bound is natural to only a few animals, e.g. some rodents, while pronk is observed in deer. If the hind legs strike together, whereas the fore feet are out of phase with each other, the gait is termed as half bound. Transverse gallop is selected by large cursors (animals with upright legs, like horse, bison etc. running medium to long distances and when running slowly. This gallop has less chance for interference between fore and hind feet, compared to rotary gallop. Rotary gallop is used by animals like cheetah and greyhound at higher speeds. It appears to be highly maneuverable. When turning, runners can change lead (precedence of individual leg on ground) during suspension. While using this gait, animals usually flex and extend the back. It benefits speed (by increasing stride length) and also helps to save energy.

There are some more gaits used by quadruped animals. For the leap in horse, no law can be formulated of universal application. While crossing a vertical wall or other obstacle, the animal gathers the feet, springs and clears the obstacle. The jump of a cat also shows greater number of variations. Lizards run in bursts of movement, stopping briefly between bursts. It may perhaps be easier for them to detect moving objects visually, while the head is stationary. Tortoise has a very slow walk during which the animal repeatedly hits the ground with its shell.

2.3. Gaits of bipeds

Compared to quadrupeds, bipeds have a relative paucity of gaits. Some primates can stand on their hind limbs and few occasionally walk in this way. One feature, which distinguishes man from his ancestors, is his bipedal form of locomotion. Based on duty factor (fraction of cycle time for

which a leg is on the ground), bipedal gaits can be classified as walk (duty factor > 0.5) or run (duty factor < 0.5). However, this classification based on duty factor is not proper for animals with more number of legs. In general, running and walking can be distinguished by the phase difference between forward horizontal kinetic energy and gravitational potential energy fluctuations. During walking, these fluctuations are out of phase whereas during running fluctuations occur in phase [8].

Human walks employ alternating periods of support by one or two legs. During periods of single support, the other leg swings forward. The relative duration of the two phases (stance and swing) depends on the speed of walk. During normal walking, the stance phase constitutes about 60% of the cycle and swing phase 40% [9]. When one leg is moving in the swing phase, the other leg is in its stance and bears the weight. Actually, the two phases overlap so that both feet are on the ground at the same time for around 20% of the cycle. As the walking speed increases, the period of double leg support decreases.

Running in both bipeds and quadrupeds generally involves at least one aerial phase in the stride. But certain variations in running including running in circles, running under enhanced gravity, running on compliant surfaces and running with increased knee flexion can reduce the aerial phase, even to zero. The absence of aerial phase does not exclude such gaits from being running because energy fluctuations in these altered gaits occur in phase [9]. During bipedal running the legs are used in strict alternation. But in bipedal hopping, the legs may be used together or with a small phase delay between foot placements.

A special gait is observed in kangaroos and probably is unique to these animals. At low speeds, the kangaroo moves by what can perhaps best be described as a pentapedal type of locomotion, since the animal uses its heavy tail as the fifth leg. This form of locomotion not only looks awkward but also appears to be energetically inefficient compared to quadrupedal running. Kangaroos change from pentapedal type of locomotion to bipedal hopping as speed increases. During hopping, stride length increases with hopping speed but hopping frequency remains constant over a three fold change in speed.

Unfortunately, there are little information on how animals move on rough and complex terrain. However, one phenomenon is clearly observed that animals have a strong tendency for posterior legs to seek support sites close to the support sites of the immediately anterior ipsilateral (same side) legs. This *follow the leader* behavior contributes to locomotion over rough terrain. During locomotion on level ground, generally, animals choose symmetric motions over the diverse range of alternatives. Perhaps, features of their mechanical structure impose constraints that make symmetric motions attractive.

3. Energetics of terrestrial legged locomotion

Muscles are biological machines for generating force. The breaking down of ATP (adenosine triphosphate) inside muscle and subsequent recombination cause contractile protein filaments to slide relative to each other. This reduces the muscle length and generates tension. Muscles are attached to the skeleton in such a way that the skeletal structure, along with muscles, form a lever system which modifies the forces produced by muscle to a great extent. Animals have both slow and fast muscles. Slow fibers are more energy efficient at low speed of contraction whereas fast

fibers are recruited at higher speed for better efficiency [10]. Muscles as well as few other elastic body parts, can store significant amount of energy elastically. Recently it is found that the work absorbed in stretching a contracting muscle can reverse the chemical process of contraction.

In order to study the energetic performance of an animal it is necessary to measure its energy consumption. One of the oldest methods is that of heat measurement. The energy that is not converted into work by the muscle is degraded into heat and can be measured using thermocouple. But, there are technical difficulties in applying the method to small animals. The most convenient and widely used method is indirect calorimetry involving the measurement of the exchange of the respiratory gases and calculating the energy equivalent. However, most muscles have the power to respire anaerobically and therefore gas exchange measurements have to be accompanied by measurements of lactate levels. The other problem is that it is not possible to know the amount of oxygen consumed for the general metabolism of the animal. The best that can be done is to subtract the oxygen consumption measurements for resting muscle from those of the exercising muscle, But this is based on the assumption that the general metabolism does not change and that all the extra oxygen is being used for the contractile apparatus.

3.1. Energetics of hexapods

There is a distinct lack of data for the invertebrates and what data is available seem fragmentary. Here, some of the important features related to hexapod energetics are discussed. Full et al. [11] made detailed study on the cockroach *Periplaneta*. It is observed that during walking front legs decelerate the center of mass whereas hind legs help to accelerate the body. Middle legs do both, much like legs in bipedal runners. Locomotion with a sprawled posture does not result in large moments around joints. Actually, production of horizontal forces during locomotion reduces joint moments by directing the ground reaction forces through the leg joints and thus reducing muscle force requirements. At higher speeds cockroaches use a posture with the front part raised, and are subjected to higher drag forces. There is a distinct increase in energy consumption at these speeds.

3.2. Energetics of quadrupeds

3.2.1. Speed of locomotion

Quadrupeds are found to use different gaits for different speeds to minimize the energy consumption for unit distance traveled [12]. The specific energy consumption, E_{sp} is measured in terms of the oxygen consumed per unit body weight per unit distance. When horses are trained in treadmill to extend a gait beyond the normal speed limits for that gait, the specific energy consumption is found to vary with speed as shown in Fig. 4. Within each gait, E_{sp} has a minimum value at *preferred speed* and represents the energetically optimal speed for that gait [13]. Transition between gaits normally occurs at the speeds where E_{sp} is the same for both the gaits. The optimum E_{sp} being nearly the same at different gaits, animals are found to keep the E_{sp} roughly constant across changes in speed and gaits [14]. One difference that was observed between larger and smaller animals is that at the speed at which gait transitions occur, the stride frequency is higher for smaller animals. McMahon [8] presented a simple model of quadrupedal gaits in which the legs were represented as springs subjected to vertical forces only and explained that animals

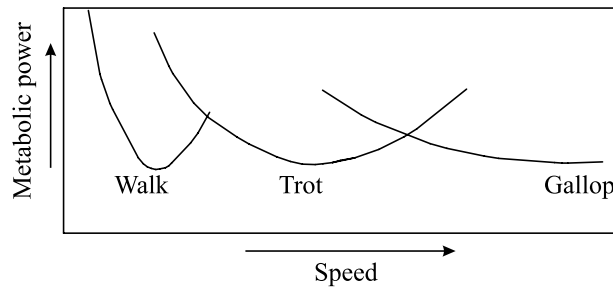


Fig. 4. Variation of oxygen cost to move unit distance against speed in horse.

change gait with speed to minimize power expenditure by adjusting leg compliance. The comparison between trotting and galloping at high speed is like the comparison between riding a steel tyred bicycle and a bicycle with high pressure pneumatic tyres. As speed increases during trotting, both the leg forces (peak as well as average) and stiffness requirement of the legs rise rapidly. The animal lowers leg forces by switching to gallop in which leg stiffness is much lower.

3.2.2. Body size

Schmidt-Nielsen [15] reviewed a remarkable range of experimental data and showed that swimming is energetically more efficient than flying, which is, in turn, more efficient than running. He observed that *specific energy consumption* (E_{sp}) decreases with animal body weight and the relationship: $E_{sp} \propto (\text{body weight})^{-v}$ is valid for all modes of locomotion; viz. swimming ($v = 0.3$), flying ($v = 0.3$) and running ($v = 0.4$). Heglund [7] explained this decrease in E_{sp} with body weight during running. He observed that the energy cost per unit body weight per stride at different speeds is about the same for all animals, independent of body size. Since smaller animals take more number of strides than larger animals, to cover the same distance, it follows that E_{sp} would be higher for smaller animals.

It is interesting to note that small animals are able to run at about the same maximum speed vertically as well as horizontally. But larger animals cannot do this. Reason behind this is the earlier stated observation by Schmidt-Nielsen that during level running, for unit distance, small animals consume much more energy per unit of their body weight compared to that of animals of larger size. It can reach as high as eight times for mouse compared to horse [16]. However, additional energy required to lift unit body weight over unit distance while running uphill is same for both the animals. The weight of small animal being much less compared to large one, the increment in energy expenditure for small animal to run uphill compared to level running, is much less compared to that for large animal.

3.2.3. Body shape

Animals cannot remain geometrically similar from the small to the large because the cross-sectional area of their limbs increases as L^2 , while body weight increases as L^3 , where L is the characteristics length of the animal. It leads to the conclusion that animals may grow no larger than a size which makes the applied stress equal to the yield stress of their materials. Animals have to either improve the strength properties of their structural materials, or modify the geometry of their musculoskeletal structure in order to grow larger. However, the strength properties of

structural materials in animal are quite similar. But, structural modifications are quite significant in some large animals. In general, animals larger than the size based on strength criteria have to increase their supporting areas directly with weight. It is widely found that some animals grow larger than others, and animals of small scale are relatively more slender than those of large scale. However, yield stress is not the only criterion [17] which determines the size and shape.

It is natural to consider that an animal can run cheaply by lightening the distal parts of the limbs and/or by concentrating the muscle mass of the limbs around their pivot joints. Otherwise, the animal has to spend significant amount of energy for alternately accelerating and decelerating the limbs. However it is observed that, despite large differences in limb configuration, the energetic cost of running in cheetahs, gazelles and goats of about same mass are nearly identical over a wide range of speeds [18]. It indicates that either the amount of energy expended in accelerating and decelerating the limbs is small compared to other expenditures or the greater limb inertia of cheetah is compensated for by greater elastic storage and recovery of energy.

3.2.4. Limb posture

The greater rate of increase of weight with size, as compared to rate of increase of limb cross-sections with size suggests that large animals have low factor of safety in their design [19]. But, it is observed that peak skeletal stresses are fairly uniform for animals ranging widely in size. Actually, similar peak bone and muscle stresses in large and small animals are achieved primarily by a size dependent change in limb posture [20,21]. Small animals have crouched postures whereas larger species are more upright. Limb muscles support and move the animal by exerting moments about the joints of the limb. The force F , the muscles must exert is determined by the equation for the balance of moments acting about the joint: $Fr = GR$, where, r is the moment arm of the muscle and R is the moment arm of the ground reaction force (G) as shown in Fig. 5. From this equation, effective mechanical advantage or EMA of the muscle as the ratio (r/R), which determines the relative magnitude of muscle force needed to counteract the external force acting about the joint. The more upright posture of larger animals increases EMA of limb muscles, enabling a reduction

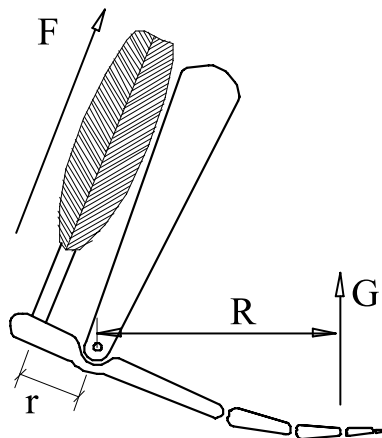


Fig. 5. Schematic illustration of EMA.

in the magnitude of muscle force requirement during locomotion. Bipedal birds (from quail to ostrich) also show a shift to more upright limb posture as size increases. EMA approaches unity in horse where muscle force and ground reaction force are of similar magnitude. It cannot be improved further once the limbs become fully upright. Due to this reason, very large animals support themselves with stout columnar limbs. The elephant is the classical example of this form of limb support. However, larger animals find it difficult to perform in postures other than the upright one, and are also more susceptible to injury due to accidental loadings.

3.3. Energetics of biped

Disagreement exists over whether man's bipedal locomotion evolved out of a need to cover long distances, or to free his hands for other functions. Surprisingly, there are no consistent differences in energy expenditure between bipedal and quadrupedal modes of locomotion [22]. Various structural adaptations behind biped locomotion occurred during the course of evolution [23]. Structure of the pelvis, development of gluteus muscles to stabilize walker's hip, upright limb configuration for improved mechanical advantage, compliant arch of foot for smooth landing and efficient take-off [24] etc. are a few of these adaptations.

The human stride demands both an up and down and a side-to-side displacement of the body. A number of functional determinants interact to move the center of gravity in space with minimum expenditure of energy. Primarily, hip, knee and foot movements working together reduce both the amplitude of the two sine like curves (up-down and sidewise) and the abruptness with which the vertical and lateral changes in direction take place [9]. If one of these elements is disturbed, an irregularity is injected into the normally smooth, undulating flow of walking. What is more important, the irregularity causes a measurable increase in energy expenditure during each step. For example, in groucho running (i.e., running with a lower position for the hip), leg compliance increases (by knee flexion) and rate of oxygen consumption is much more compared to that of normal running [25]. It is due to the increased forces in anti-gravity muscles of the legs caused by the changed mechanical advantage of the muscles.

During walking each leg works as an inverted pendulum. This form is energetically economical because it allows for the exchange of gravitational potential and kinetic energy of the body. While moving at uniform speed on level ground, people and animals perform a small quantity of net work (to overcome friction and air resistance) by doing large quantities of positive work and almost equal quantities of negative work. However, they minimize positive work requirement by aligning foot forces roughly in line with their legs [25]. The foot force slopes backward, tending to decelerate the animal during the first half, and slopes forward, tending to accelerate the animal in the second half of stance. Thus the positive work requirement of the muscles is reduced in walking by the principle of an inverted pendulum.

Human running and bipedal hopping of kangaroo and some small mammals (for example, hopping mice) are reminiscent of a bouncing ball. Horizontal kinetic energy and gravitational potential energy fluctuate in phase. A significant amount of energy expended in a step remains stored in elastic body parts and is recovered in the subsequent step. Stride frequency as well as energy cost per stride remain almost constant [26] as speed increases (primarily by increasing the stride length). Hopping in kangaroo is the most inexpensive mode of locomotion at high speeds

due to the greater elastic storage and the subsequent recovery of energy. However, for small hoppers, probably, the chief benefit of this mode is related to enhancement of abilities to escape from predators [27]. However, elastic body elements are ineffective in walking. During walking, the leg exerts large force when it hits the ground as well as when it pushes off. Between these events, it exerts less force and thus cannot retain any strain energy gained during impact to power the push off.

Not only bipeds but all animals using bouncing gaits (hopping, galloping, bipedal running etc.) can store part of the energy expended, in elastic body elements like muscles, tendons, ligaments etc. at one stage of the stride and release later through elastic recoil to reduce overall energy expenditure [28,29]. These gaits also make significant use of bending of the back to increase step length as well as to store elastic strain energy. Kangaroo during bipedal hopping, stores as much as 50% of the energy requirement elastically in tendons, ligaments of rear limbs and tail during impact with the ground to release later as the animal rebounds for next hop. Some insects have power amplifier similar to catapult mechanism and helps to release power rapidly for jumping.

One important aspect to note in legged animal design is symmetry with respect to longitudinal body axis. Perhaps, animals use symmetry to simplify control. However, in legged animals, all legs are not identical. It is due to the differences in requirement imposed upon them. For example, for insects and quadrupeds, hind legs propel the body forward whereas front legs work to decelerate the body.

4. Conclusion

Animals use a variety of gaits. Hexapods, with their larger number of legs, are able to walk with static stability and also retain significant mobility in case of accidental removal of one or two legs. Though a wider variety of gaits were expected in the hexapods (because of more number of legs), the maximum variety is observed in quadrupeds. Quadrupeds systematically switch from one gait to another while changing speed to maintain economy in energy expenditure. Quadrupeds require dynamic stability at higher speeds, while bipeds require it at all speeds.

It is observed that animals cannot remain geometrically similar from the small to large due to similar strength properties of their structural materials. Larger animals support their relatively higher body weight by using the upright limb postures which allow better muscle force transmission characteristics. However, this leads to a restriction in postures and accidental loadings are more fatal to them. The energy cost of transport per unit body weight is much less for large animal compared to small one. But, small animals have almost equal mobility while moving on level ground as well as uphill.

Despite differences in body size, body form, type of skeleton, number of legs and leg orientation, animals exhibit remarkable similarity in their locomotor mechanics. All use two basic mechanisms for minimizing energy expenditure for locomotion. During walking, animal's center of mass rises and falls, kinetic and gravitational potential energy are exchanged rather than lost in a manner analogous to swinging pendulum. While running, animals use a second mechanism to alternately store and release energy in elastic body elements in a manner analogous to what occurs in a bouncing ball.

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