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Stability During Arboreal Locomotion

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1. Introduction

Arboreal locomotion – traveling on the branches, twigs, and trunks of trees and woody shrubs – is very common among mammals. Most primates, many rodents, marsupials, carnivores, and even an occasional artiodactyl travel on arboreal substrates to forage, escape predators, and acquire shelter. Arboreal supports are usually far enough from the ground that a slip or fall could cause serious injury or death, or deprive the animal of a mate, food, or energy. Thus, stability is of great importance for an animal traveling on arboreal supports. The considerable variation among arboreal supports makes stability during locomotion a mechanical challenge. Supports vary in diameter, slope, compliance, texture, direction (that is, bends or curves in a branch), and number and distribution. Furthermore there may be interaction among these variables; for example, compliance varies with diameter – thinner branches are more compliant than thick branches. Also, the thin branches frequently have leaves that act like sails in the wind, causing even more movement in the substrate. Substrate texture often varies with diameter, where narrow twigs have smoother bark than large branches or trunks. Therefore one might expect a considerable number of morphological, behavioral, and biomechanical mechanisms to enhance stability on arboreal supports.

Stability can be divided into two categories: static and dynamic. Static stability is the process by which objects at rest remain stable, i.e., neither move (translation) nor rotate about a point or axis. For example, a table is statically stable because the forces and moments (torques) produced by gravity (weight) are balanced by ground reaction forces and the moments generated by them. One way an animal might remain stable is by not moving and adhering to or gripping the support; this definition is the ultimate example of static stability in an animal. Although this strategy allows no movement, it is nevertheless a valid locomotor strategy for an animal attempting to travel on an arboreal support subjected to a sudden gust of wind or other disturbance (Stevens, 2003). This analysis also applies when the animal walks very slowly, but fails when it walks or runs at considerable speed. Because the distribution of the mass is changing from one instant to the next, the forces and torques necessary to maintain static stability would also change with time. That is, it requires an active control by the nervous system. Because stability is critical, it is very likely that the animal employs both active and passive control (Full et al., 2002). Passive control can be due to dynamic processes of the animal's body, and is referred to as dynamic stability. For example, a hiker might cross a stream or river by running across a fallen log; the rotation of the limbs around the hips and shoulder

generates a gyroscopic effect. This gyroscopic effect helps prevent the hiker from toppling off the log. In this chapter we will review the mechanics of static stability during arboreal locomotion. We will then expand on the mechanics of dynamic stability and its importance in arboreal locomotion.

2. Static stability

Slow lorises, as their name implies, usually move very slowly (although see Nekaris and Stevens, 2007). One of the mechanisms these primates use to avoid toppling from narrow arboreal supports is the same method used by the table. At all times the center of mass of the table or slow loris is supported by three or four legs, making toppling less likely (Fig. 1; Hildebrand, 1980).

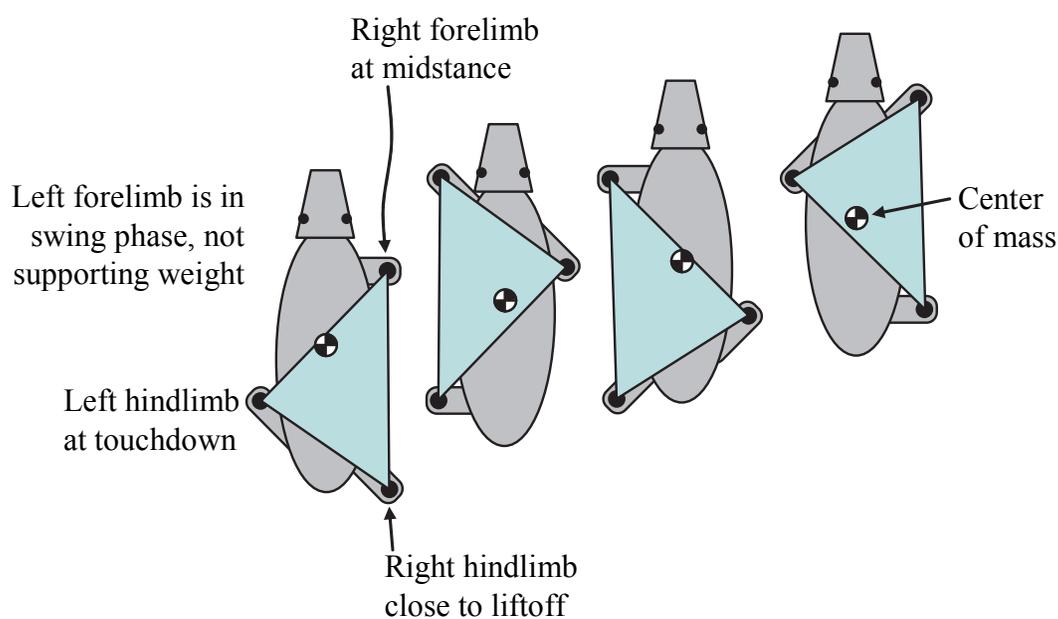


Fig. 1. Base of support (blue triangles) generated by the limbs in contact with the ground or substrate (based on Hildebrand, 1980). The footfall pattern illustrated here is a lateral sequence singlefoot gait (left hind, left fore, right hind, right fore, with footfalls spaced fairly evenly in time). The duty factor is approximately 75%. Note that the center of mass (black and white circle) is supported by three limbs at all times.

Footfall pattern can affect whether the center of gravity passes through the polygon of support. First, at slow speeds, the duty factor usually increases (Fig. 2). Duty factor is the duration of time that a foot or hand contacts a substrate divided by the total stride cycle time. A duty factor of 100% indicates a hand or foot that never leaves the substrate (therefore no movement occurs); a zero duty factor means the animal is flying. Intermediate duty factors indicate how much time within each stride a hand or foot is in contact with the substrate. At slow speeds, when duty factor is high (Fig. 2), the likelihood is higher that three or four limbs are in contact with the substrate at any given moment. Three or four limbs create a support polygon through which the center of gravity may pass, maintaining stability against toppling due to the acceleration of gravity on the animal's mass. However if the branch the animal travels on is very narrow, then the support polygon may be so narrow

that the center of mass is frequently outside the polygon. When this occurs, the weight of the animal will create a torque that can make the animal topple.

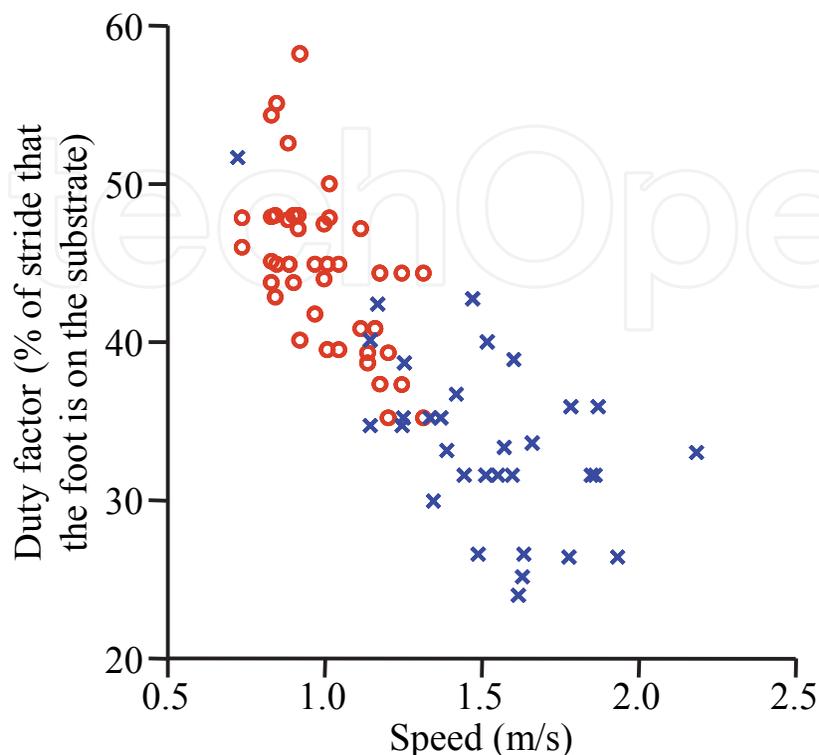


Fig. 2. Duty factor versus speed for gray short-tailed opossums walking and running on branches (red circles) and a flat trackway (blue Xs).

The sequence of footfalls can also affect where the center of gravity falls within a support polygon (Fig. 1). The variation in footfall patterns among taxa, the possible adaptive benefits of different footfall patterns, and the relationship of footfall patterns and walking/running mechanics are elaborated upon by Hildebrand (1976, 1980), Cartmill et al., (2002, 2007), and Reilly and Biknevičius (2003). When animals walk, trot, or pace, the right and left hindlimbs and right and left forelimbs are perfectly out of phase (Fig. 3). For example: assume a stride begins at the time of right lower extremity touchdown, and ends just before the next touchdown of the same limb. At the time the person's right lower extremity touches down while walking, the left lower extremity is halfway through the stride cycle. This also occurs with the right/left hindlimbs and forelimbs of quadrupeds. The phase relationship (limb phase) between the right hindlimb and right forelimb (or left hind and left fore) can be compared as a percentage of synchronization (Fig. 3). For example, if the right hindlimb and forelimb are synchronized (footfall and liftoff occur at the same time), the limb phase is 0%, and the animal is pacing. During a trot, the limb phase is 50% and the right forelimb is 50% ahead or behind whatever the right hindlimb is doing. During a lateral-sequence gait, the limb phase is between 0-50%. (Note: in this chapter, the word *gait* means footfall pattern, which is the definition typically used for non-human locomotor biomechanics. For human locomotor biomechanics, *gait* is any locomotion). After a right hindlimb lands, the right forelimb is the next limb to land. During this gait the center of gravity always passes through the support polygon (as long as three or four limbs are in contact with the ground). The diagonal-sequence gait features a limb phase between 50-100%. After a right hindlimb

lands, the *left* forelimb is the next to land. This gait has frequently been observed among arboreal primates, the marsupials Monito del Monte and woolly opossum, and the carnivore kinkajou (Pridmore, 1994; Schmitt and Lemelin, 2002; Lemelin and Cartmill, 2010), although not in the arboreal sugar glider (*Petaurus breviceps*; Shapiro and Young, 2010). The prevalence of diagonal-sequence gaits among arboreal quadrupeds, and the strong lack of prevalence among terrestrial animals, demands an explanation. Cartmill et al. (2002, 2007) suggest that the diagonal sequence gait is an adaptation for increasing stability while walking on narrow arboreal supports. They demonstrate that the diagonal sequence diagonal-couplets gait increases the likelihood that opposing limbs will simultaneously grip the narrow arboreal support (Cartmill et al., 2002, 2007) instead of ipsilateral limbs (limbs on the same side of the body). An animal using this gait will follow a hindlimb contact with a forelimb contact on the opposite side (thus, diagonal sequence). If the hindlimb and diagonal forelimb strike the substrate closely in time, the diagonal sequence gait is also a diagonal couplet gait. Furthermore, Lemelin and Cartmill (2010) point out that the diagonal sequence diagonal couplet gait maximizes the spatial distance between contralateral limbs, which might limit the vertical oscillation of the center of mass. When the opposing limbs of a diagonal sequence diagonal couplet gait (or a trot) apply medially-directed force (Schmitt, 2003; Lammers and Biknevicius, 2004; Schmidt and Fischer, 2010), they squeeze the branch and increase normal force. Friction force is therefore increased, which makes slipping less likely. Furthermore, opposing mediolateral impulses and angular impulses generated by opposing limbs might reduce the mediolateral deviation from the long axis of the branch (Shapiro and Raichlen, 2007). It is also possible, however, that the prevalence of diagonal sequence gaits among many arboreal taxa results from differences in duty factor and stance durations between fore- and hindlimbs (Stevens, 2006).

It is also possible that the stability of an arboreal animal could be affected by the running gait it uses. During *bounding* locomotion, the forelimbs land simultaneously, followed by simultaneous contact of the hindlimbs (or vice-versa). If hindlimbs land simultaneously, but the forelimbs land at separate times, such a gait is referred to as a *half-bound*. A *gallop* is where forelimbs and hindlimbs land at different times; it differs from the gaits described in previous paragraphs (e.g., lateral sequence gait) because although the right and left hindlimbs (or right and left forelimbs) do not land at the same time, the hindlimb footfall contacts both occur before the forelimb contacts occur (or forelimbs can both land before hindlimbs; Bertram and Gutmann, 2008). During any footfall, energy is transmitted from the body of the animal to the substrate. If the animal runs on a narrow branch, the transfer of energy could cause the branch to oscillate, which could destabilize the running animal. Bertram and Gutmann (2008) suggest that a gallop, with its four separate footfalls, can reduce the amount of energy imparted to the ground or branch. We therefore predict that when an arboreal animal's mass relative to branch diameter is substantial enough to cause a branch to oscillate and destabilize the animal, that animal will run with a gallop or half-bound instead of a bounding gait. This prediction is supported by data presented by Young (2009), who showed that running marmosets and squirrel monkeys increase the lead time between right and left limb pairs when running on a narrow cylindrical trackway. For example, if the left forelimb lands first, the time interval (relative to stride duration) between left forelimb and right forelimb touchdowns is greater on the arboreal trackway. It appears that increasing duty factor and crouching during walking gaits has a similar effect of decreasing the vertical oscillation of a narrow arboreal support. Schmitt (1999) found that a

wide variety of arboreal primates crouch and walk with a large duty factor, which reduces the peak vertical force and vertical oscillation of the branch; Young (2009) found similar results among running marmosets and squirrel monkeys.

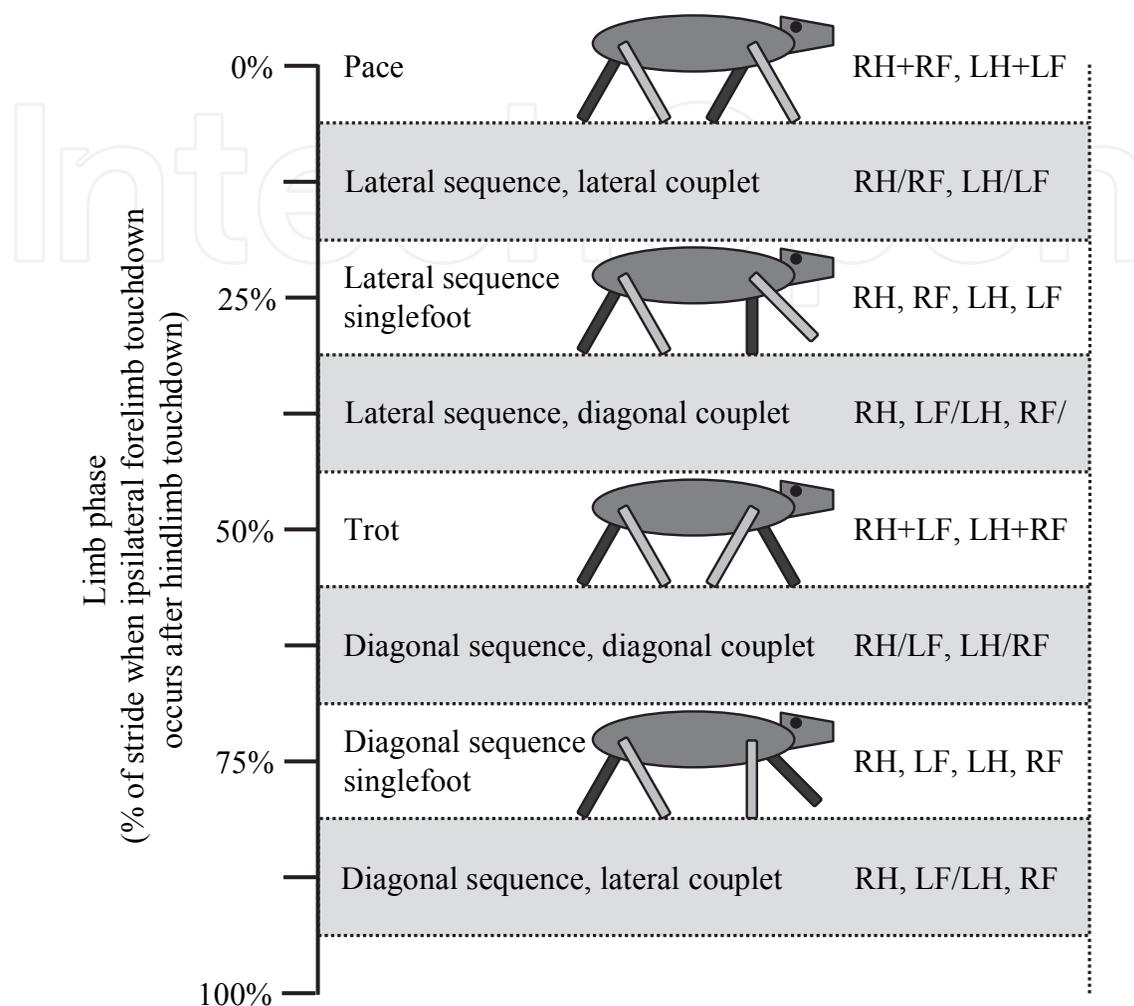


Fig. 3. Limb phase. Note that the configuration of the hindlimbs is the same in each drawing, and that the timing of the forelimb footfalls differs. Right limbs are shown as light gray and left limbs are dark gray. To the right of the quadruped drawings are footfall sequences (R = right, L = left, H = hindlimb, F = forelimb; + indicates footfalls occurring simultaneously, / indicates footfalls occurring close together in time, and a comma designates footfalls occurring relatively far apart in time. In the lateral sequence and diagonal sequence singlefoot gaits, all four footfalls are more or less evenly spaced in time. Each of the eight footfall patterns is defined by a limb phase (e.g., 25%) \pm 6.25%. See Hildebrand (1976, 1980) for further detail.

Many arboreal primates, the woolly opossum, and the kinkajou reduce the vertical oscillation of the center of mass while walking on branches (Schmitt, 1999; Schmitt and Lemelin, 2002; Schmitt et al., 2006; Young, 2009; Lemelin and Cartmill, 2010). A gait frequently employed to reduce vertical oscillation is the *amble*, first termed by Schmitt et al. (2006). During ambling locomotion, the duty factor is less than 50% and the footfall pattern is trot-like or diagonal sequence, but there is no aerial phase. In other words, at least one

foot is always in contact with the substrate. The lack of an aerial phase means that the center of mass is limited in its dorsal and ventral accelerations, which reduces peak vertical force, which in turn should reduce the vertical oscillation of thin branches (Young, 2009). The effects of branch oscillation or compliance on locomotor kinematics or kinetics are largely unexplored. Stevens (2003) demonstrated that primates change the movements of the limbs very little when a horizontal artificial branch trackway was oscillated in dorsoventral or mediolateral directions. However when the branch underwent twisting (rotating around the long axis), the quadrupedal primates stopped walking and appeared to freeze while branch movement was occurring (Stevens, 2003). Such rotational movement in thin branches could occur during strong winds, with the foliage acting like a sail.

The height of the center of mass over the substrate only matters when the gravitational acceleration vector passing through the center of mass (that is, the center of gravity) falls outside the base of support created by the limbs. The probability of this occurring decreases if the animal crouches. If the center of gravity *does* leave the base of support, then gravitational acceleration acts on the mass, creating a force. The horizontal distance between the center of mass and the outside of the base of support multiplied by the force is a torque that could cause the animal to topple from the support. There are at least three possible solutions (Cartmill, 1985):

1. Generate an opposing torque or other compensation; this requires a strong grip using opposable digits or opposing limbs. The tail may also contribute to reducing the total moment at any given instant (Larson and Stern, 2006).
2. Hang upside-down under the branch; in doing so, the animal will not fall as long as its grip on the branch (via opposable digits, opposable limbs, or both) does not give out. But now the world appears upside down, and the animal must either exert constant force with its musculature, or possess anatomy that allows the grip to be maintained with claws and/or a locking mechanism.
3. Reduce the length of the moment arm by crouching. (Cartmill, 1985, also points out that toppling moment can be reduced over evolutionary time by decreasing overall body size).

Many arboreal taxa grip the supports with long fingers and toes, including an opposable thumb and/or hallux (Cartmill, 1972, 1974, 1985). Strong gripping allows the animal to exert powerful torques on the branch, and the reaction torques stop the animal from toppling off the sides of the branch (Cartmill, 1985). (Strong gripping and exerting torques to keep the center of mass within the base of support formed by the limbs could also be classified as *dynamic stability* because the torque and gripping forces may need to be adjusted as the animal moves). To avoid slipping, arboreal taxa must increase friction force or generate some form of adhesion. Many arboreal taxa have claws to create new contact surfaces that allow normal force to be more efficiently generated (Cartmill, 1985). Some increase friction via pads that possess dermatoglyphic ridges (fingerprints) or other complex micro-structures that interact with the substrate to increase friction force (Cartmill, 1974; Hamrick, 2001). Suction, capillary action, or dry adhesion are other ways that an arboreal animal can make slipping less likely (Cartmill, 1985; Autumn et al., 2006).

The condition of static equilibrium depends on the details of the footfall pattern, details of the anatomy, and the direction and magnitude of the substrate reaction force and torque. This means that the force and torque components necessary for the condition of static stability at one instant during a stride would not provide stability at any other instant.

Therefore the condition of static stability will, in general, be violated except at very slow speeds. Thus another mechanism – dynamic stability – is responsible for the animal's stability when the forces and torques are not fully balanced.

3. Dynamic stability

Dynamic stability can be divided into two categories for analysis: the interaction of the whole, moving body with the substrate, and the internal movements of the various body parts (rotation of the hindlimbs around the hip joints or flexion and extension of the torso, for example). As the whole body moves over an arboreal substrate, the substrate reaction forces act to rotate the body around the center of mass (except during the instances where the substrate reaction force passes directly through the center of mass). Thus the body rotates around the roll, yaw, and pitch axes (Lammers and Zurcher, 2011). Any rotation of the body will increase the likelihood of toppling from a narrow support, especially rotation around the roll axis (around the anteroposterior or craniocaudal axis). Therefore it is necessary that a moment rotating the body in one direction (rolling to the left, for example) is balanced by a moment rolling the body back to the right. This can be quantified by integrating torque or moment during step time (angular momentum or angular impulse). As long as the angular impulse averaged over a stride is zero (or nearly zero), the rotational dynamics prevents the toppling of the animal and it will remain stable. Some data suggest that net zero angular impulses are often not maintained within a single stride, and that two or more strides are necessary to maintain dynamic stability (Belli et al, 1995; Forner-Cordero et al., 2006; Lammers and Zurcher, 2011). Another caveat with maintaining net zero angular impulses is that *at any instant*, it is necessary that moment is non-zero (positive or negative). The condition that the sum of the forces and moments about the center of mass over a stride is tiny or zero is not sufficient to maintain stability because the equilibrium configuration can either be stable, unstable, or indifferent/neutral (Fig. 4; Full et al., 2002). In an unstable equilibrium condition, non-zero moments must be applied to maintain stability. An example of this condition is riding a bicycle.

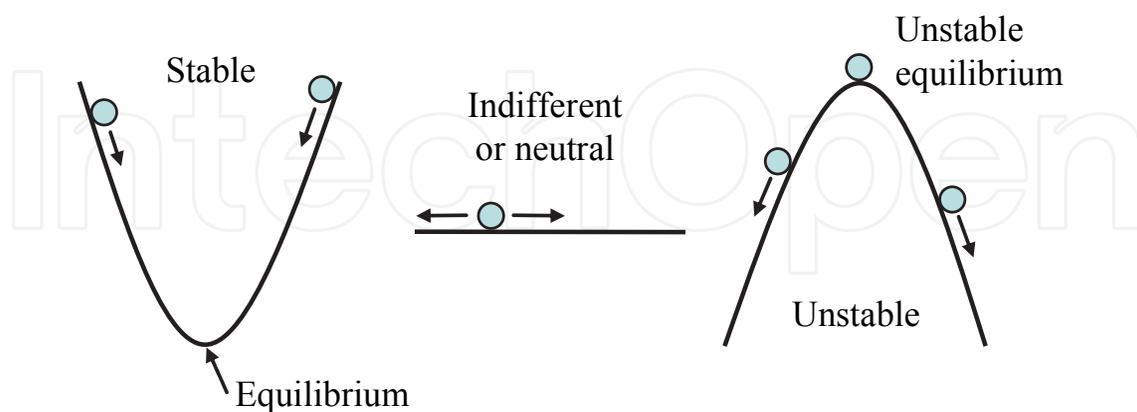


Fig. 4. In the stable configuration, a ball always rolls toward the equilibrium point at the bottom of the valley. In the indifferent or neutral configuration, the ball can roll anywhere and remain equally stable or unstable. In the unstable equilibrium condition, the ball is stable only if it remains perfectly balanced at the top of the hill. (See Full et al., 2002, for further detail).

In the static case, a person sitting on a bicycle will not topple if the person and bicycle are perfectly aligned along the vertical. However the person will fall if he/she and bicycle deviate even slightly from the upright position. On the other hand, a person riding a bicycle does not have any difficulty navigating even a rough terrain. This dynamic stability of the bicycle originates from the angular momentum of the wheels. The wheels rotate about their axis so that their angular momenta are approximately horizontal and perpendicular to the forward motion. If the bicycle is tilted away from the vertical position, the weight exerts a non-zero moment in the horizontal plane and directed in the forward direction. This moment drives the system back towards the equilibrium position. This is sometimes referred to as the “gyroscope effect.” The vector of the angular motion of the wheels rotates, or precesses, about the vector of the angular momentum with the angular frequency Ω (Fig. 5). The spinning of the wheel provides a *constant angular momentum* for the bicycle. There is, of course, no analogue of a spinning wheel for animal locomotion. For dynamic stability during arboreal locomotion, the non-zero angular momentum stems from small distortions

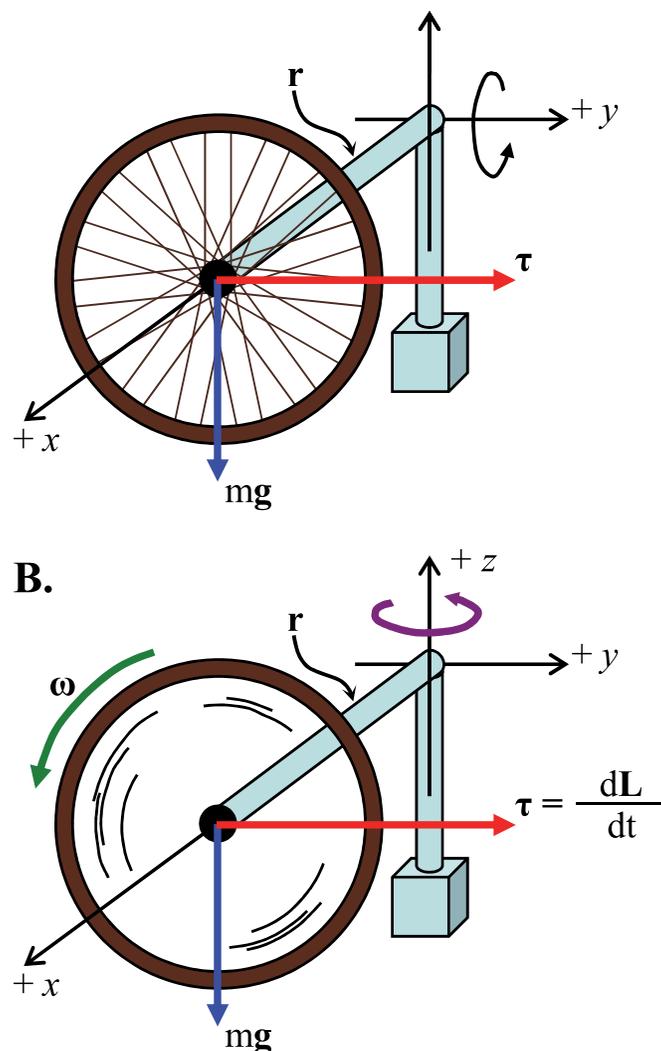


Fig. 5. A., a non-spinning bicycle wheel falls around axis y because mg exerts torque τ . B. When the bicycle wheel spins, it precesses around the z axis because of angular momentum L . (Adapted from Goldenstein, 2001).

of the animal's body. This includes the rotation of the limbs around the hip joint or center of rotation of the scapula; it is possible that the flexion and extension of the animal's trunk during galloping or bounding locomotion can also be included as a source of angular momentum. In human locomotion the angular momentum is due largely to the pendulum motion of legs and arms so the angular momentum must be different in the first and second half of a stride. In this manner, the *average* angular momentum during a stride is (approximately) zero. Indeed, Herr and Popovic (2008) analyzed the role of angular momentum in human walking, and found it to be highly regulated during a stride. The average angular momentum is nearly zero in all three spatial dimensions, but follows a distinct pattern during different phases that contributes to the stability. They found that angular momentum is important for the dynamic stability of human locomotion. Because the mass of the limbs of many quadrupedal arboreal animals (relative to their overall body mass) is small, the pendulum-like motion of the limbs might produce only a small angular momentum. For example, each forelimb of the Siberian chipmunk comprises about 4% of the total body mass, and hindlimbs are each about 6%. However many quadrupedal arboreal primates *do* possess relatively massive fore- and hind limbs, with much of the mass concentrated at the distal ends (Raichlen, 2006). Arboreal primates rely heavily on grasping hands and feet (Cartmill, 1972), and Raichlen (2006) suggests that the distal concentration of muscle mass contributes to the ability of primates' grasping ability. We agree with Raichlen (2006), but we suggest that the distal mass concentration also has the effect of increasing arboreal stability via increased angular momentum of the limbs.

4. Modeling

In the following, we use the convention that vector quantities, e.g., velocity, are printed in bold face. To use our model, we collected kinematic data from Siberian chipmunks (*Tamias sibiricus*) running on a cylindrical trackway 2 cm in diameter. The chipmunks were videotaped using two high-speed video cameras (210 Hz). Each camera captured a different view, and we then used the APAS motion analysis system to digitize 14 points on the head, body, tail, and the right forelimb and hindlimb. Thus we obtained a dataset of 14 three-dimensional points which described the position of the head, body, tail, and limbs every 210th of a second. We chose trials where the chipmunks bounded so that right and left limb pairs were moving more or less synchronously, and their position and movement is symmetrical on either side of the sagittal plane. Using estimates of segment masses obtained from a dead specimen, each segment is assigned a mass (m_i) with coordinate vectors $\mathbf{r}_i(n)$ at the time t_n . Thus the motion of each segment (e.g., body segments, limb segments, etc.) can be described. The digitized coordinates between consecutive video frames determine the coordinate vectors. The velocity vectors are then obtained: $\mathbf{v}_i(n) = [\mathbf{r}_i(n+1) - \mathbf{r}_i(n)] / \Delta t$, where $\Delta t = t_{n+1} - t_n$.

The center of mass [$\mathbf{R}_{CM}(n)$] is then found:

$$\mathbf{R}_{CM}(n) = \frac{\sum_i m_i \mathbf{r}_i(n)}{\sum_i m_i} = \frac{\sum_i m_i \mathbf{r}_i(n)}{M},$$

where M is the total mass. In the following notations, we suppress the discrete time dependence [that is, we eliminate the term n to make the expressions less cumbersome; e.g., R_{CM} rather than $R_{CM}(n)$]. The total linear momentum (P) is:

$$P = MV_{CM} = \sum_i m_i v_i,$$

where V_{CM} is the velocity of the center of mass. The relative coordinates and velocities are defined,

$$\begin{aligned} r_i &= R_{CM} + \delta r_i, \\ v_i &= V_{CM} + \delta v_i, \end{aligned}$$

where δr_i and δv_i are coordinate and velocity vectors with respect to the center of mass. The total angular momentum (L) has a contribution from the center of mass motion and the relative motion of the body segments (Goldstein et al., 2001).

$$L = R_{CM} \times MV_{CM} + \sum_i \delta r_i \times m_i \delta v_i$$

When the center of pressure falls beyond the substrate, the animal is less likely to topple if the angular momentum around the mediolateral axis induces a precession-like rotation of the animal around the vertical axis.

Our preliminary data from Siberian chipmunks running on a narrow (2 cm diameter) cylinder (Fig. 6) suggest that the movement of the head and torso generates very little rolling angular momentum, and that it is largely centered around the zero axis (that is, above the central axis of the cylindrical trackway). Pitch and yaw momentum are relatively large. The pitch momentum results from the flexion and extension of the body, which should contribute to the gyroscopic effect. The yaw momentum is quite unexpected. We noticed that the chipmunks often ran on the left side of the branch trackway, perhaps to avoid the lights or experimenters. The large pitch angular momentum observed here is supported by data from Lammers and Zurcher (2011), which were obtained via a force pole and digitized 240 Hz videography (Fig. 7). Our data show that pitch angular momentum (the area enclosed by the pitch torque versus step time plot) is considerably greater than yaw and rolling angular momenta.

Full et al (2002) argue that neural control best enhances stability when it works with the natural, passive dynamics of the mechanical system. Our preliminary results show that the relative motion of the head, body, and limbs of the chipmunk generate the angular momentum, and thereby replace, partially at least, the role of legs and arms for human locomotion. We believe that the gyroscope effect associated with a non-zero angular momentum is critical for the initial response to a sudden external perturbation (e.g., sway or jerking of a branch) before the hands and feet have a chance to change their grip. Such a passive control is essential for the stability of the animal because it prevents the center of mass from deviating too much outside the base of support. Otherwise the body weight could produce a torque that is too large to be balanced by torques produced by substrate reaction forces and torques generated by the limb musculature.

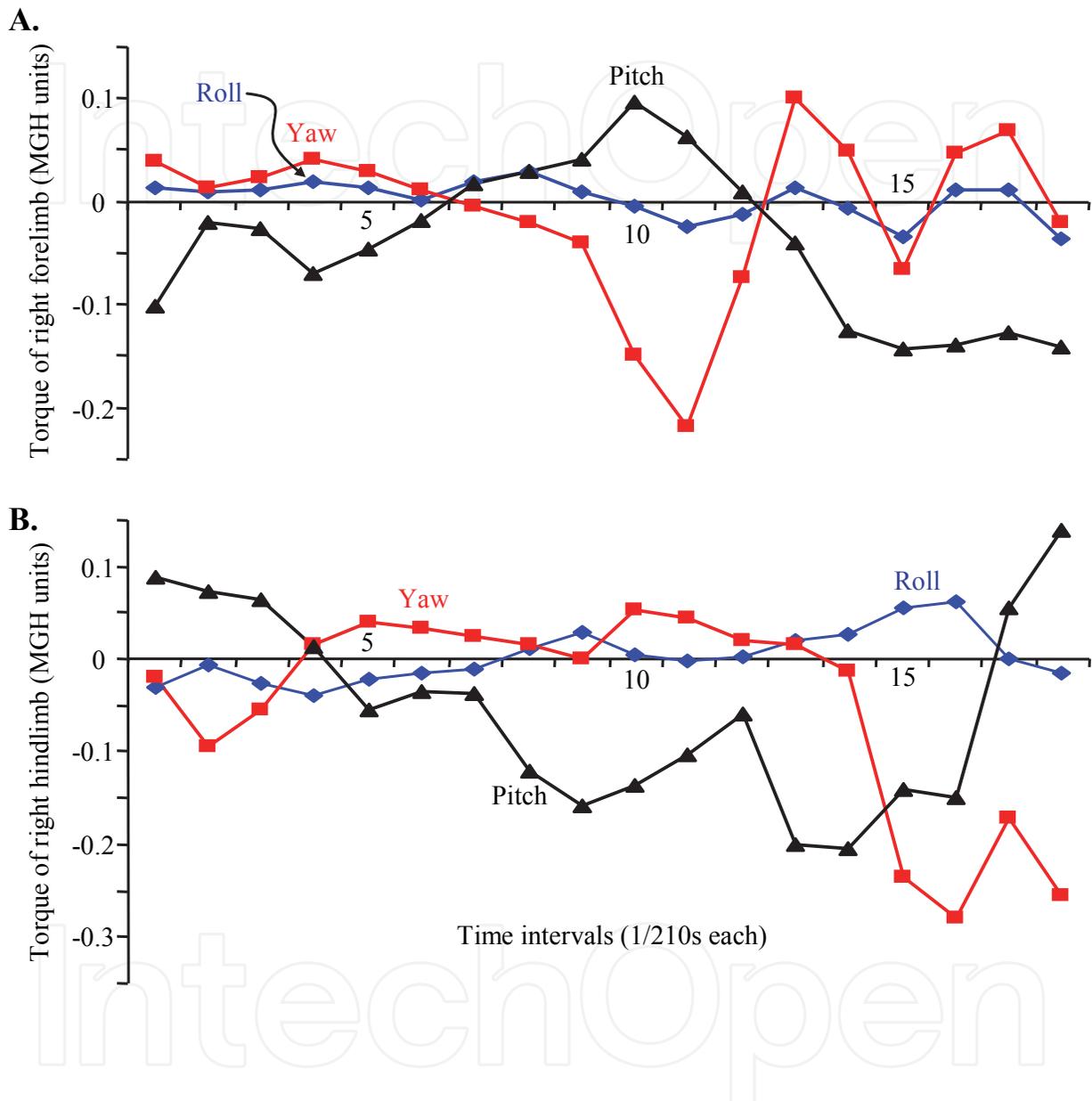


Fig. 6. Torque around three axes during one stride of the Siberian chipmunk. A, right forelimb; B, right hindlimb. Blue triangles represent pitch torque (around a mediolateral axis); red squares represent yaw, and black diamonds are rolling torque. The data points are smoothed by using a moving average; points 1 and 2 are averaged, then 2 and 3, etc. The portions of the stride where yaw torque is large are the swing phases of the limbs, where the limb most likely moves laterally and medially more than during stance phase. Pitch torque reflects the flexion and extension of the limbs and body. Rolling torque remains relatively small.

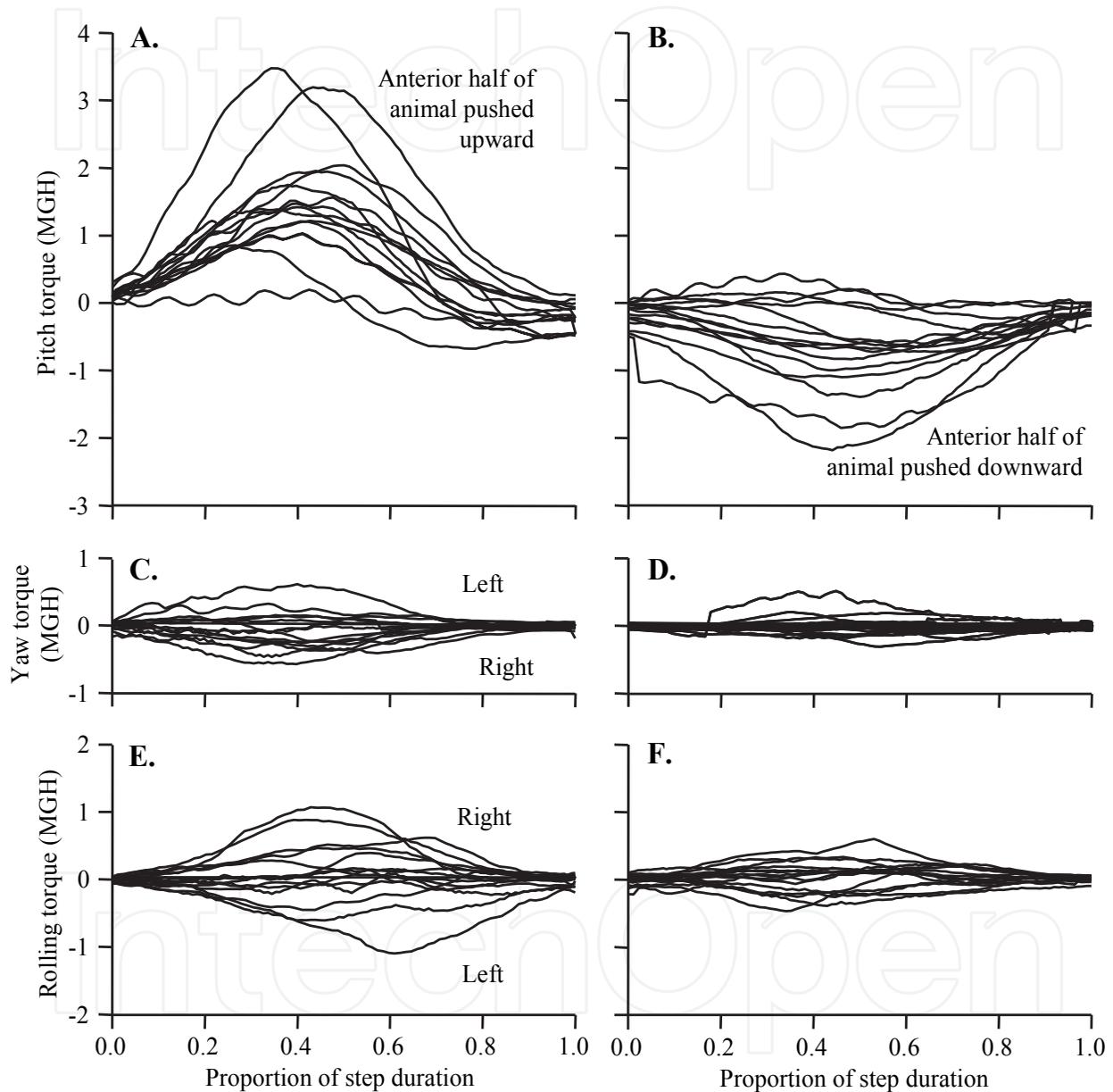


Fig. 7. Torques (MGH = mass · acceleration of gravity · center of mass height) around the center of mass versus percent of step time during forelimb contacts (A, C, and E) and hindlimb contacts (B, D, and F).

5. Dynamic stability analysis

We discuss two different methods of stability analysis. First, we consider only the angular momentum of the center of mass without considering the mass and velocities of the individual parts (L'):

$$L' = R_{CM} \times MV_{CM}.$$

Some aspects of the dynamic stability of a bicycle can be used to understand stability during arboreal locomotion. Replacing total angular momentum L with the term L' from the center of mass motion would correspond to a bicycle sliding on a frictionless surface. The wheels do not spin, and the bicycle is mechanically unstable. The body is easily perturbed – if the center of pressure of the hand or foot of the animal or the wheel of the bicycle falls outside the support, a fall or stumble will probably occur. The system (arboreal mammal or bicycle) is dynamically stable if all internal degrees of freedom are included (that is, the mass, positions, and movements of each segment). Here we can add or subtract different modeled parts of the animal to determine their contributions to the angular momentum (and hence, to the dynamic stability):

$$L'' = R_{CM} \times MV_{CM} + \sum_{i \neq k, l, m, \dots} \delta r_i \times m_i \delta v_i.$$

In the expression above, the angular momentum of the center of mass *and* the angular momenta of individual parts are taken into account, but we can remove body segments, tail segments, limbs, etc. to determine their contribution. The second term $\delta L = \sum_{i \neq k, l, m, \dots} \delta r_i \times m_i \delta v_i$ provides the necessary angular momentum so that the animal's

center of mass precesses around the vertical axis, and thereby prevents the animal from falling from the branch.

The second type of stability analysis uses tools to investigate the stability of dynamic systems for which the underlying equations of motion are not known (Strogatz, 1994). This method is based on the time-dependence of the dynamic variable Q at discrete times t_n , $Q = Q(n)$. For the present study, either the craniocaudal or mediolateral component of the angular momentum are useful choices for the quantity Q . In the phase portrait, the quantity $Q(n+1)$ at time t_{n+1} is plotted versus the same quantity $Q(n)$ at time t_n . If we choose $Q = L_{CC}$ (angular momentum around the craniocaudal axis), the phase portrait will consist of approximate circles, which is the signature of oscillatory motion. Circles in the phase portrait are referred to as “limit cycles” in the mathematical description of dynamic systems. Because the angular momentum (in this example, around the craniocaudal axis of the animal and the branch trackway) maintains a cycle, dynamic stability is maintained. Mathematical tools have been developed to quantify the stability of the system from limit cycles. This method has been used by Blickhan and coworkers (e.g., Seyfarth et al., 2002) to quantify the dynamic stability of human locomotion.

6. The impact of understanding stability during arboreal locomotion

Understanding how arboreal animals utilize static and dynamic stability during arboreal locomotion can provide insights to engineers attempting to build robots with legs.

Biologically-inspired robots might use dynamic stability strategies rather than static stability (Ritzmann et al., 2004). Also, the evolution of an arboreal animal's morphology, behavior, and central nervous system probably assumes dynamic stability mechanisms are used at high speed. This is especially true among animals whose center of mass is relatively far from the ground or substrate. The limb posture of primitive tetrapods was considerably less upright than many modern mammals (including humans); thus we expect that dynamic stability mechanisms were less important to such sprawling animals. A thorough grounding in the importance of dynamic stability during locomotion might help to understand the anatomy and function of motor control systems and brains in general.

7. References

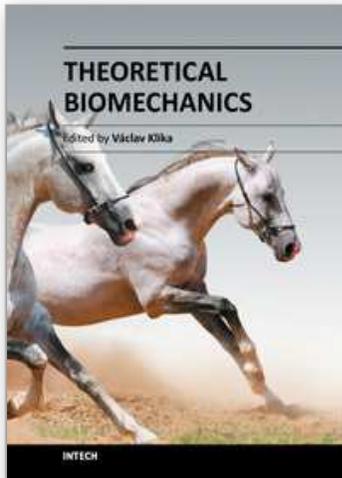
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Theoretical Biomechanics

Edited by Dr Vaclav Klika

ISBN 978-953-307-851-9

Hard cover, 402 pages

Publisher InTech

Published online 25, November, 2011

Published in print edition November, 2011

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How to reference

In order to correctly reference this scholarly work, feel free to copy and paste the following:

Andrew R. Lammers and Ulrich Zurcher (2011). Stability During Arboreal Locomotion, Theoretical Biomechanics, Dr Vaclav Klika (Ed.), ISBN: 978-953-307-851-9, InTech, Available from:
<http://www.intechopen.com/books/theoretical-biomechanics/stability-during-arboreal-locomotion>

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