7 Locomotion and positional behavior of spider monkeys
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Introduction
Living atelines form a unique group that occupies an important place in the adaptive radiation of New World monkeys. The four (or five) genera, Alouatta, Ateles, Lagothrix (and Oreonax) and Brachyteles, that compose the group are distinguished from other platyrrhines by their relatively large size (c. 5–11 kg), strong inclination to herbivory (fruits and leaves), tail-assisted forelimb-dominated suspensory positional behavior with associated postcranial morphology, and a prehensile tail with a naked ventral grasping surface (Rosenberger and Strier, 1989; Strier, 1992). Although consistent in its phylogenetic unity, atelines are morphologically and behaviorally heterogeneous.

More precisely, howler monkeys, Alouatta spp., appear to have opted for an energy minimizing foraging strategy, feeding on high proportions of leaves through sitting and tail–hindlimb assisted postures, and exploiting small home ranges traveling short daily distances mainly by quadrupedally walking and clambering above branches (Rosenberger and Strier, 1989; Strier, 1992). On the other hand, the rest of the genera, grouped as atelins, appear to share several derived features related to more agile and suspensory locomotor and postural behaviors as well as a more energy maximizing foraging strategy (Rosenberger and Strier, 1989; Strier, 1992). Phylogenetic relationships between these genera have not been established yet, especially under the light of new data deriving from molecular studies (Harada et al., 1995; Schneider et al., 1996; Cavanez et al., 1999; von Dornum and Ruvolo, 1999; Meireles et al., 1999; Collins, 2004). Based on ecomorphological and behavioral data, woolly monkeys Lagothrix, appear to be the more primitive atelin, whereas spider monkeys Ateles, and woolly spider monkeys Brachyteles are considered as a highly derived group, sharing postcranial adaptations to agile tail-assisted forelimb suspensory locomotion, similar energy expenditure foraging strategies, and fission–fusion societies (Rosenberger and Strier, 1989; Strier, 1992). In contrast, molecular data, deriving from the study of many different loci, have produced...
identical results grouping *Lagothrix* and *Brachyteles* together and leaving *Ateles* as a sister group to the former (Harada et al., 1995; Schneider et al., 1996; Cavanez et al., 1999; von Dornum and Ruvolo, 1999; Meireles et al., 1999) or even unresolved trichotomy (Collins, 2004; see also Rosenberger et al., this volume).

These differences, although contradictory, provide fertile ground for reconsidering the values and weights of different sets of data (Hartwig, 2005). These arguments are further supplemented by the rich fossil material (complete skeletons of *Caipora* and *Protopithecus*) that provides new insights into the evolution of morphological traits in atelines, within and/or outside assumed ecomorphological complexes. Among such complexes, positional behavior (i.e. locomotion, postures, manipulation), the way body weight is transferred across substrates, the active maintenance of immobility, and the way food items are collected and processed to mouth, may play a significant role in inferring and interpreting the interrelationships between historical and functional factors that shape morphology, as well as the adaptive significance of behavioral ecology. In effect, positional behavior is a signal of the constant and versatile interaction between the architecture of the postcranium and that of the surrounding environment. When quantified, well described and analyzed, positional behavior can provide a strong basis for interpreting homoplasies and homologies within evolutionary scenarios (Lockwood, 1999).

Among platyrrhines, atelines have enjoyed a relatively large number of studies of positional behavior. This is mainly because the postcranial morphology of the group is repeatedly compared to that of early anthropoids (Fleagle and Simons, 1982) and Miocene hominoids (Rose, 1996). More particularly, the positional behavior of *Ateles* especially has received much attention both in quantitative analysis of positional behavior in the wild (Mittermeier, 1978; Fleagle and Mittermeier, 1980; Cant, 1986; Fontaine, 1990; Bergeson, 1998; Cant et al., 2001, 2003; Youlatos, 2002; Campbell et al., 2005), as well as kinematic and kinetic analyses of selected frequent and critical positional modes (see previous papers and Turnquist et al., 1999; Hirasaki et al., 2000; Isler, 2004; Schmitt et al., 2005). This chapter aims to review the available data and to provide stimuli for further and more focused research on the positional behavior of *Ateles* in the field.

**Locomotor and postural modes performed by Ateles**

In order to study the positional behavior of *Ateles* and its evolution in association with postcranial morphofunctional correlates, there is a need to know exactly how extant ateline species locomote in the wild. Different modes have been defined in different ways across observers and this requires a clarification
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of this system by detailed description, kinematic (and kinetic) analysis, and tests of performance of the different positional categories. This will aid in two ways. A detailed analysis of definition of modes will help in the comprehension of eventual differences between Ateles species or field sites. Second, each species appears to execute each mode in a different manner. Therefore lumping categories together may mask subtle differences that can be crucial to the understanding of adaptive variability and evolutionary trends. Although there has been an attempt to standardize applied definitions of modes used in studies of positional behavior (Hunt et al., 1996), most researchers tend to use their own system mainly for the sake of comparability. For these reasons, I shall initially compare the terminology applied to describe the modes that compose positional categories and provide a kinematic analysis where available based on both field and laboratory research.

Leap and drop

Leaping and dropping involve an airborne phase and are the main means of crossing gaps across the canopy. Leaping is used for crossing gaps that are longer than an animal can navigate with other, more secure, means. In leaping, the horizontal component of the airborne phase is usually longer than the vertical one, and functions as a rapid way to cross tree crowns or within-tree sites. Leaping requires the action of rapid and simultaneous extension of the hindlimbs in order to provide the necessary thrust for propelling the body. Initiation may be from a moving or a stationary position, above or below one or multiple supports. Most takeoffs are initiated from above a support by adopting a quadrupedal fast or slow progression or an analogous posture. When below the support, forelimb-assisted progression is usually the predominant takeoff mode. During the airborne phase, the animal usually assumes the spread-eagled position, but other postures may be used (Mittermeier, 1978). Direction of the body displacement can be upward, horizontal or downward. However, in all cases the horizontal component is more important than the vertical displacement of the body. Most leaps cover distances between 2 and 5 m, rarely longer (Mittermeier, 1978; Fontaine, 1990; Cant et al., 2001). Landing usually takes place above the support, by adopting a quadrupedal stance, where the forelimbs land first. Below support landing is also common and usually terminates with a tail–forelimb-assisted suspensory posture or progression (Fontaine, 1990; Cant et al., 2001).

In dropping, the vertical component of the airborne phase is longer than the horizontal one. Thus, dropping serves for rapid downward vertical displacement within the canopy. Dropping usually lacks propulsive effort from the hindlimbs
and usually initiates from a position above or below the take-off support. When above the support, the animal assumes a quadrupedal or bipedal posture or a cautious quadrupedal or bipedal progression. Suspensory takeoffs are more frequent (Fontaine, 1990; Cant et al., 2001) and usually involve a combination of forelimbs, hindlimbs, and the tail. Tail-assisted forelimb and tail-only suspension appear to be the most common takeoff modes (Fontaine, 1990) and are passive as the animal simply leaves the grasps. During the airborne phase the animal assumes the spread-eagled position, and it can be either head- or tail-first. Dropping usually covers relatively short vertical distances between 1 and 3 m (Fontaine, 1990; Cant et al., 2001). In most cases, landing occurs above the support, with the hindlimbs touching the landing support first, waiting for the stabilization of the flexible supports to continue progression.

**Bipedalism**

Bipedal activities mainly involve bipedal walk and assisted bipedal walk, where forelimbs and the prehensile tail help support the orthograde stance of the body. During this infrequent mode, which occurs mainly on medium-sized horizontal or subhorizontal supports (Mittermeier, 1978; Cant et al., 2001) and on the ground (Campbell et al., 2005), progression is relatively slow. There is significant flexion and abduction of the thigh, and when it is forelimb assisted, the knee is importantly flexed.

**Quadrupedalism**

Quadrupedalism or quadrupedal activities are variably defined in different studies. Mittermeier (1978), in his study of *A. geoffroyi* and *A. paniscus*, limited quadrupedal activities to quadrupedal walk and run involving diagonal or lateral gaits on relatively stable horizontal or inclined supports. Fontaine (1990), in his study of *A. geoffroyi*, included quadrupedal walk, bound, slow bound, gallop, and run as well as tripod and bound in his category of quadrupedal locomotion, and all these modes were described similarly to Mittermeier’s. However it is not clear as to whether these modes occur only on single or multiple parallel-sided supports and not on multiple intertwined ones. Similarly, in the study of *A. belzebuth belzebuth* in Ecuador, the quadrupedal locomotion described by Cant et al. (2001) involved quadrupedal walk along single or multiple more or less parallel horizontal supports utilizing all four limbs, in a slightly or highly flexed posture, in a diagonal sequence. Following the same lines, in my study of *A. paniscus* in French Guiana (Youlatos, 2002), I also separated quadrupedal
walk and run from other locomotor categories. In contrast, the quadrupedalism of Cant (1986) stands out as it appears to incorporate quadrupedal walk and run on single horizontal supports, as well as all climbing activities on vertical single supports, and thus included all quadrupedal activities irrespective of support orientation.

In all cases, quadrupedal walk along single horizontal or subhorizontal supports (Figure 7.1a) involves a diagonal sequence in *Ateles* (Youlatos, 1994). The gait appears to provide locomotor stability on relatively unstable supports, by ensuring that the hind foot grasps in a protracted position on a known substrate at the moment when the contralateral forefoot touches down on a new substrate (Cartmill et al., 2002). Hindlimbs are usually the first to leave and touch down on the support (Vilensky, 1989; Cartmill et al., 2002). The hip joint is maintained adducted and progressively extends throughout the support phase, aided by the constant firing of the adductor magnus (Fleagle et al., 1981). Abduction is minimal and reaches a maximum at the mid-swing phase. The knee does not show complete extension prior to touchdown. In the hind foot the toes touch the substrate first and are subsequently followed by the heel (Schmitt and Larson, 1995). The foot either grasps or poses itself laterally upon the substrate, depending on its size. Excursion in the shoulder joint is ample, reaching a minimum in the propulsive phase and a maximum at touchdown, when the forelimb is also slightly abducted during touchdown (Stern et al., 1980a, 1980b; Schmitt, 1994; Larson et al., 2000). Propulsion is provided by the recruitment of several extrinsic scapular muscles, such as the trapezius, serratus and pectoralis major, that pull the body forward relative to the supported forelimb (Stern et al., 1976, 1980a, 1980b; Fleagle et al., 1981; Konstandt et al., 1982). Arm abduction is especially pronounced during the mid-swing and mid-support phases (Schmitt, 1994). The elbow joint is usually kept semi-extended during the support phase, but reaches particularly extended positions prior to touchdown when a new farther reach is attained (Schmitt, 1994; Larson, 1998a, 1998b; Larson et al., 2000), at which point the body is primarily supported by the active firing of the triceps muscles (Fleagle et al., 1981). The forearm is variably positioned during the support phase. In most cases, the forearm is pronated and the hand is posed in a palm down position and laterally deviated on the substrate depending on its size (Lemelin and Schmitt, 1998). In contrast, in phases when the forearm is maintained supinated, a hook-like grasp is used around the underside of the support. In all cases, the wrist is passively hyperextended during the mid-support phase (Schmitt, 1994). On small flexible substrates (e.g. lianas or terminal branches), a crouched form of quadrupedal walk is assumed. This is referred to as “compliant walking” and protraction, flexion and abduction of the forelimb and hindlimb joints are more pronounced, providing a longer and more stable reach, improving balance on unstable substrates, and reducing peak
Figure 7.1 Locomotor modes in *Ateles belzebuth* and *A. paniscus*: (a) quadrupedal walk, (b) clamber, (c) brachiation, and (d) bridging.
reaction stresses (Schmitt, 1999; Schmitt and Hanna, 2004). In such instances, both diagonal and lateral gaits can be used, the latter mainly as transitional (Youlatos, 1994).

Vertical ascent and descent

When substrates deviate from the horizontal or subhorizontal plane, most authors tend to recognize a separate locomotor mode – vertical climb (contra Cant, 1986). Mittermeier (1978) and Fontaine (1990) included what
they termed “quadrupedal climbing” in their climbing category. I recog-
ized a similar mode, defined as vertical climb (Youlatos, 2002). In con-
trast, Cant et al. (2001) recognized two separate modes depending on the
inclination of the used support and termed them as “vertical and oblique
ascent” respectively, but included them in a separate ascend/descend locomotor
category.

Vertical climbing is characterized by diagonal sequence/diagonal couplets
(Isler, 2004), where the foot leaves the support first, followed by the contralat-
eral forelimb. Three limbs usually provide support (Isler, 2004) and the tail
is rarely used (Youlatos, 2002). Substrate characteristics appear to influence
footfall patterns, and vertical climbing on large diameter supports is mainly
performed by lateral sequences (Isler, 2004). Cycle duration and relative stride
lengths are long, with that of the forelimb being longer (Hirasaki et al., 1993;
Isler, 2004). In effect, the arm, with aid of middle serratus and middle deltoid,
is raised well above the shoulder to reach a new and higher hold (Stern et al.,
1980a, 1980b; Fleagle et al., 1981) and the elbow may fully extend prior to
touchdown. During support, the elbow is flexed on thin substrates, while fully
extended on larger ones (Isler, 2004) and shows a momentary peak of flexion
mainly in early support phase (Hirasaki et al., 2000). The elbow joint appears
to act in flexion throughout the support phase, while it extends passively in the
late support phase (Fleagle et al., 1981; Hirasaki et al., 2000). The wrist
shows an abduction peak in the late support phase (Hirasaki et al., 2000),
while the hand uses a hook-like prehension around the substrate. In general,
kinematic and electromyographic analyses of muscle recruitment, during the
support phase, provide evidence that the major role of the forelimb is to keep
the body close to the substrate (Stern et al., 1976, 1980a, 1980b; Hirasaki et al.,
2000). In contrast, the hindlimb plays a preponderant role in pushing the ani-
mal off and providing thrust for propulsion (Fleagle et al., 1981; Hirasaki
et al., 2000; Isler, 2004). In general, hindlimb joints exhibit greater excursions
than forelimb ones, probably in order to reduce joint moments (Hirasaki et al.,
1993). In addition, the hip and knee joints act mainly in extension and may
be abducted (Hirasaki et al., 2000). The ankle acts primarily in plantar flexion
(Hirasaki et al., 2000) and the foot is characterized by strong prehension while
the heel never touches the support. Lastly, it appears that total muscle power
in the hindlimb peaks in the late support phase, most likely related to intense
muscle activity that is important for the push-off phase (Hirasaki et al., 2000).
In fact, the climbing style of Ateles resembles that of hominoids, and more
particularly the bonobo, Pan paniscus, and appears to be quite efficient requir-
ing less energy than other quadrupedal monkeys (Hirasaki et al., 2000; Isler,
2004).
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Clamber

When spider monkeys move on various directions along and across multiple variably oriented supports, Cant (1986) defines it as clambering, but transitional, which is a mode between clambering and the initiation of tail-assisted forelimb suspension. The former mode is termed as “horizontal climbing” by Mittermeier (1978), and involves climbing on a roughly horizontal plane upon flexible supports, combining quadrupedal walk and suspensory posturing. On the other hand, Fontaine (1990) most likely includes it within the quadrupedal walk category. Cant et al. (2001) recognize several clambering modes related to the direction of body displacement along the network of the multiple flexible supports, as well as the adopted posture (orthograde or pronograde). Lastly, I recognize clamber as a separate locomotor mode but have included all directions of body displacement and postures within the same category (Youlatos, 2002).

By definition, clambering in various directions occurs on multiple supports that are intertwined in variable orientations (Figure 7.1b). During progression, there is no particular gait as limbs grasp hold of the available supports. The body can be directed upwards, horizontally, or downwards. The elbow and knee joints are frequently under complete extension and abduction, especially during the stance phase. The forelimb is usually placed above the shoulder level during the swing phase depending on support availability. The hindlimb grasps the support via the toes and the heel does not contact the support. Hand grasps are hook-like. On fewer occasions, the body is held orthograde and both forelimbs and tail support the posture during progression. The arms are usually raised above the shoulder showing significant extension and abduction. The hindlimbs appear to support the body weight and may be under complete knee extension, especially prior to touchdown. Abduction and flexion at the thigh can be also significant. In all directions and postures, the tail is used often (Cant, 1986; Youlatos, 2002) and is placed primarily above the animal, most certainly supporting part of the body weight. No detailed analysis exists of tail use during clambering bouts but comparable data of tail use in tail–arm brachiation (Schmitt et al., 2005) imply a significant and active role.

Bridge

Mittermeier (1978) and Cant (1986) distinguish bridging as a mode closely related to horizontal climbing (or clambering) that is used during crossings between tree peripheries. Bridging begins by securing the initial supports and
grasping the terminal supports, followed by pulling them over, and finally climbing across the terminal supports (Figure 7.1d). Grasping of terminal supports is mainly achieved by an incomplete leap, but bridging never involves an airborne phase. I also define bridging in a similar manner without distinguishing any finer categories that involve body direction or initiation method (Youlatos, 2002). Fontaine (1990) identifies two different bridging modes based on direction of body crossing: descending bridging which involves a tail-hindlimb suspensory posture between primary and terminal supports, and pronograde bridging. In contrast to previous authors, the study of Ecuadorian *A. belzebuth belzebuth* identifies many bridging modes that are grouped under bridge/hoist locomotor category (Cant et al., 2001). All these modes are defined the same way as previous authors, but are distinguished by the direction of the movement, as well as the relative placement of the body. Bridging represents a significant proportion of the traveling locomotion of *A. b. belzebuth*, but the dominant modes are pronograde horizontal and downward oblique bridging. Furthermore, bridging is the dominant mode for crossing gaps in the canopy. In all studies, the frequency of bridging behavior, which incipiently involves traversing of many tree crowns, is significantly reduced during feeding locomotion.

Irrespective of the direction of the movement during bridging, the mode always involves the use of the prehensile tail that grasps firmly on a support above the animal and bears initially part, but finally the whole of the body weight prior to the grasping of the terminal supports. In all cases, the forelimbs leave the initial supports first, are usually characterized by frequent abduction and extension at the elbow, and are raised well above the shoulder. The forearm appears to be under considerable pronosupinatory rotation and the hands anchor the terminal supports by a hook-like grasp. In many cases, bridging is initiated by a lunging movement, but never involves an airborne phase. More precisely, there are at least two limbs secured at any time, the tail excluded. The hindlimbs leave the initial support last and are usually under adduction and complete extension at the thigh and knee, and plantar flexion at the ankle joint.

**Suspensory locomotion**

*Atelidae* engages in a variety of suspensory modes of locomotion. The most common ones are tail-assisted forelimb swing and tail-assisted brachiation (Figure 7.1c), with tail swing, inverted quadrupedal walk and inverted clamber being used less frequently.

Tail-assisted forelimb swing is described as suspensory progression using alternating forelimbs that may be held in an extended or partly flexed position at the elbow joint during the support phase. Trunk rotation is absent or particularly
Limited and the tail is frequently, but not always, used; however, when in use it may grasp behind the trailing hand, or between hands. In this mode it is possible that only the initially trailing forelimb swings forward to take a grip, whereas the initially leading forelimb remains in place. In this case, Cant et al. (2003) identify a separate mode, the half-stride forelimb swing.

Tail-assisted brachiation is a more dynamic and usually faster form of forelimb swing that involves a trunk rotation of over 180 degrees between hand contacts (Jenkins et al., 1978; Jenkins, 1981). Half-stride brachiation, when only the initially trailing forelimb swings forward to take a grip, while the initially leading forelimb remains in place, can also occur, but trunk rotation also remains close to 180 degrees. Half-stride suspensory locomotion is relatively uncommon in Ateles (Cant et al., 2003). Ateles also engages in ricochetal brachiation that usually involves variable periods of noncontact between handholds. This suspensory mode is less frequently used, but can be much faster, as horizontal velocity is supposed to remain constant during the ballistic aerial phase, resulting in an increased forward speed, providing access to farther handholds by means of an unusual pendulum that has substantially more kinetic than potential energy (Preuschoft and Demes, 1984; Bertram, 2004).

Tail-assisted brachiation, forelimb swing, and inverted quadrupedalism have been identified as separate modes in most studies of positional behavior of Ateles, although the latter mode has been given different names (Mittermeier, 1978; Youlatos, 2002; Cant et al., 2003). Only Cant (1986) included tail-assisted brachiation and forelimb swing under his tail–arm-suspension category, and identified a separate one, “transitional,” that can be placed somewhere between tail-assisted forelimb suspension and clamber.

The way tail-assisted brachiation is performed by Ateles has been well documented in both the wild and under laboratory settings. Detailed analysis of videos shot in the wild in both French Guiana and Ecuador show that brachiation is usually employed below and along one or sometimes across multiple supports. The body is usually held relatively orthograde, but body position largely depends on tail use and the placement of the tail hold (Turnquist et al., 1999). It appears that Ateles keeps the body relatively pronograde mainly due to the consistent and active use of the prehensile tail (Turnquist et al., 1999). However, the more horizontal body postures in Ateles appear to be associated with the addition of potential energy within the brachiating system, in a different way from that observed in brachiating hylobatids (Turnquist et al., 1999). In addition, lateral body sway is lowest when the tail grasps the substrate (Schmitt et al., 2005). The tail is capable of retarding and lifting the body (Jenkins et al., 1978) and its liftoff precedes that of the leading hand (Turnquist et al., 1999). In effect, the tail grasps behind the trailing hand or between forelimbs, and is used with every other handhold, resulting in a more flowing progression...
The active recruitment of the tail in tail-assisted brachiation kinematics in *Ateles* appears to be related to its capacity of hyperextension that is functionally associated with certain osteomuscular features such as its length, longer proximal caudal region, more acute sacrocaudal angle, and wider transverse processes (Lemelin, 1995; Schmitt et al., 2005). This results in significant differences in forelimb joint kinematics between tail use and nonuse. The forelimbs are raised well above the shoulder, particularly when the tail is simultaneously engaged, whereas shorter excursions are observed when not using the tail (Turnquist et al., 1999). The morphology of the shoulder girdle allows the efficiency of the swing, by engaging in scapular rotation, and caudal and medial translation (Jenkins et al., 1978). This morphology, in combination with complex muscle recruitment (Stern et al., 1976; 1980a, 1980b; Fleagle et al., 1981; Konstandt et al., 1982), permits a caudal and medial shoulder movement towards the median plane and appears to facilitate the dynamics of pendular swinging (Jenkins et al., 1978; Schmitt et al., 2005). In addition, the elbows are only partially extended when the tail grasps, whereas higher values of elbow extension are encountered when the tail is not used (Turnquist et al., 1999). The forearm engages in ample pronatory and supinatory movements that appear to be facilitated by mid-carpal rotation during the support phase (Jenkins, 1981; Jungers and Stern, 1981). In fact, in *Ateles* these distal rotatory movements appear to be responsible for rotation of the trunk (Jenkins, 1981). During tail-assisted brachiation, the trunk always displays a great rotation between hand contacts (Jenkins et al., 1978). In addition, strides are relatively high in length and duration, with long support and swing phases, as well as relatively short free flight phase per stride duration (Turnquist et al., 1999). In higher speeds, both swing and support phase duration decrease, resulting in an insignificant reduction of the duty factor. This pattern is supposed to accommodate longer periods of contact and thus to reduce peaks of substrate reaction forces, as in primate quadrupeds (Turnquist et al., 1999). Initiation of a brachiation bout can be from above, below or the same level as the substrate and termination can be in a suspended position below the support, in a supported position above the support, or on top of a lower support. The fluidity of these movements as analyzed under controlled conditions and as observed under real naturalistic conditions in the canopy demonstrates that *Ateles* can perform, readily and proficiently, long bouts of tail-assisted brachiation with variable periods of free flight. This mode may be energetically efficient and may provide shorter travel routes within the canopy (Parsons and Taylor, 1977; Cant, 1986, 1992). On the other hand, *Ateles* appear to use a different pendular system of energy storage and use, but are kinematically closer to hominoids than the other atelin brachiators (Turnquist et al., 1999; Bertram, 2004).
Supported postures

Among the anthropoids the seated posture is the most frequently used (Rose, 1974). While sitting, the weight of the animal is usually supported by either the ischia or the hindlimbs (Figure 7.2f). Most studies fail to distinguish between these two categories, grouping together all sitting observations into one major mode, termed as sit (Mittermeier, 1978; Cant, 1986; Fontaine, 1990). Youlatos (2002) and others (D. Youlatos, J. G. H. Cant, and D. M. Rose, unpublished data) distinguish two modes: (a) sit or ischial sit where the majority of the animal’s weight is born by the rump and the hindlimbs may be either flexed or extended; (b) squat or nonischial sit, where the animal sits at right angles to the
length of the substrate, while the extremely flexed hindlimbs firmly grasp the substrate and no weight is born by the rump. In both cases, extra stabilization may be provided by any combination of forelimbs and tail.

In both quadrupedal and tripod stand the body is held pronograde and mainly parallel to the substrate. Contact with the substrate is provided by firm grasps of both hands and feet. When one forelimb is not in contact with the supportive substrate(s) the posture is defined as tripod. This hand may be either free, manipulating a food item, or providing additional support upon another substrate, which is not in parallel with the supportive substrate(s).
Most studies classify both postures under stand (Mittermeier, 1978; Bergeson, 1998; Youlatos, 2002) or distinguish between tripedalism and quadrupedalism (Fontaine, 1990). D. Youlatos, J. G. H. Cant and D. M. Rose (unpublished data) further discern these postures on the basis of limb flexion, which implies the action of applied forces upon the supportive limbs. When both forelimbs and hindlimbs are substantially flexed in elbows and knees, the posture (either quadrupedal or tripedal) is identified as crouch. This posture allows the animal to stand closer to the substrate and very likely provides an equilibrium advantage. The posture represents variable proportions of the above substrate postural repertoire of spider monkeys but appears to be the second more frequent supported posture.

When only the hindlimbs support the body weight, the standing posture is defined as bipedal stand and is seldom used by Ateles (Mittermeier, 1978; Cant, 1986; Fontaine, 1990; Bergeson, 1998, Youlatos, 2002). The feet may be either posed on the substrate or engaged in a firm grasp. The body may be held
Figure 7.2 (cont.)
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Figure 7.2 (cont.)
Either orthograde or semipronograde. Additional support may be provided by a combination of forelimbs and tail. In this case, the forelimbs may be actively involved, holding the substrate under tension, or they may be simply placed upon a substrate at the level of the body, stabilizing the posture of the animal. When the knees are substantially flexed, D. Youlatos, J. G. H. Cant and D. M. Rose (unpublished data) distinguish a different mode referred to as bipedal crouch.

Vertical cling is a posture that occurs on vertical and subvertical substrates, and is characterized by the attachment of the animal by all four limbs. The body is held orthograde and parallel to the substrate and the tail may or may not provide additional support, grasping either above or below the animal on the same substrate or one that is nearby. All limbs are highly flexed and act to maintain the body close to the substrate. Clinging postures are identified in most studies (Mittermeier, 1978; Fontaine, 1990; Bergeson, 1998; Youlatos, 2002; D. Youlatos, J. G. H. Cant and D. M. Rose, unpublished data) but contribute insignificantly to the overall postural repertoire of *Ateles*.

Recline, lie and sprawl incorporate a variety of supported postures where the body, either pronograde or supinograde, is supported by the substrate. These postures are seldom used during feeding activities (Mittermeier, 1978; Youlatos, 2002; D. Youlatos, J. G. H. Cant and D. M. Rose, unpublished data) but are extensively adopted during short or long resting sessions (Fontaine, 1990). This variety of postures is usually grouped under recline (Mittermeier, 1978) or lie (Youlatos, 2002), but Fontaine (1990) and D. Youlatos, J. G. H. Cant and D. M. Rose (unpublished data) distinguish detailed categories, in respect with the side of the body that is in contact with the substrate (ventral, dorsal, flank, etc.) and the position of the limbs.

**Suspended postures**

*Ateles* exhibits a remarkable variety of suspended postures that involve several combinations of forelimbs, hindlimbs and the tail. The latter is always used during suspensory postural behavior and depending on the posture may or may not play a primary role.

Tail-only hang is commonly used by *Ateles*. In this posture, the tail exclusively supports the entire weight of the body (Figure 7.2d). The body may be held either vertically downward, with the hindlimbs particularly flexed at the hips, or at an angle, with the hindlimbs held somewhat behind the suspended animal. The forelimbs may be hanging free or manipulating food items or holding twigs that are found at a level which is lower to the center of mass of the animal. Most
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authors recognize this posture as a separate mode (Cant, 1986; Fontaine, 1990; Youlatos, 2002; D. Youlatos, J. G. H. Cant and D. M. Rose, unpublished data).

Tail–hindlimb hang involves the action of the tail and one or both hindlimbs (Figure 7.2a). This posture appears to be used extensively among atelines (Schönybarra, 1984; Cant, 1986; Gebo, 1992; Bergeson, 1998; Youlatos, 1998; D. Youlatos, J. G. H. Cant and D. M. Rose, unpublished data). The hindlimbs are under tension, and the foot is particularly plantar flexed. The hip and knee are extended and can be variably abducted. Most authors distinguish a tail–hindlimb hang posture, and Fontaine (1990) goes even further to distinguish tail–one-hindlimb-hang and tail–two-hindlimb hang.

Horizontal tripod is a posture that employs the tail and the two hindlimbs, the former being under tension, while the latter are pressed against the substrates and are under compression (Figure 7.2e). In this posture, the body is usually held more or less pronograde or at an acute angle to the horizontal. The tail grasps above the animal but the hindlimbs are usually positioned below the level of the rump. The hindlimbs are usually extended and adducted at the hip joint, but can be either flexed or semiextended at the knee. Cant (1986) initially identified the posture as tripod; Youlatos (2002) and others (D. Youlatos, J. G. H. Cant and D. M. Rose, unpublished data) use the same term, whereas Fontaine (1990) and Bergeson (1998) use the term “inverted bipedal” to describe it.

Tail–forelimb hang is a relatively common feeding posture in Ateles. The tail grasps above the animal and one forelimb grasps in full extension below the same or a nearby substrate (Figure 7.2c). Depending on the relative position of the two grasping points, the body is usually held pronograde and only rarely orthograde. Conversely, tail–two-forelimb hang is a common posture during short-term or long-term resting. During this posture, the tail grasps beside the grasping forelimbs that are both extended and may be either abducted or adducted at the shoulder. In this case, the trunk is held more or less pronograde as in tail–forelimb hang.

Tail–forelimb–hindlimb hang is similar to tail–forelimb hang, with the exception that one foot grasps on the side, so that the trunk of the animal faces partly to that side (Figure 7.2b). The forelimb is usually abducted at the shoulder, and extended at the elbow. The hindlimb is particularly abducted and extended at the hip, while extended at the knee. A strongly plantar flexed and distally inverted foot secures hindlimb grasp; however, this posture is not very common in Ateles (D. Youlatos, J. G. H. Cant and D. M. Rose, unpublished data).

Lastly, a quite uncommon posture is quadrupedal hang, when all forelimbs and hindlimbs are involved in supporting the suspended supinograde trunk. The limbs may be suspended below the same or different substrates, and the tail may or not be grasping above the animal. Mittermeier (1978) indirectly describes the posture when he considers the use of all five limbs, in his analysis of limb
D. Youlatos

Table 7.1 Summary of percentages of gross locomotor categories in positional studies of three species of Ateles

<table>
<thead>
<tr>
<th>A. geoffroyi</th>
<th>A. paniscus</th>
<th>A. belzebuth</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site</td>
<td>Panama</td>
<td>Guatemala</td>
</tr>
<tr>
<td>Method</td>
<td>wet bout</td>
<td>dry 10-sec</td>
</tr>
<tr>
<td>Quadrupedal</td>
<td>22.0%</td>
<td>52.0%</td>
</tr>
<tr>
<td>Climbleamber</td>
<td>24.2%</td>
<td>19%</td>
</tr>
<tr>
<td>Bridge</td>
<td>4.6%</td>
<td>4.0%</td>
</tr>
<tr>
<td>Suspended</td>
<td>25.7%</td>
<td>25.0%</td>
</tr>
<tr>
<td>Airborne</td>
<td>10.9%</td>
<td>1.0%</td>
</tr>
</tbody>
</table>

1: Mittermeier (1978); 2: Cant (1986); 3: Fontaine (1990); 4: Youlatos (2002); 5: Cant et al. (2001).

use in suspensory postures, and it is also described by Fontaine (1990) and Bergesosn (1998).

Positional behavior and profile of Ateles in the wild

Thus far, the positional behavior of Ateles has been the subject of several quantitative studies. These studies, although they have used different methodologies of data collection and mode definition, and were carried out in different sites during different periods, have provided quantitative data for three different species (Tables 7.1 and 7.2). The Central American spider monkey (A. geoffroyi) has been studied in both wet tropical forest in Barro Colorado Island (BCI), Panama (Mittermeier, 1978; Fontaine, 1990) and Costa Rica (Bergeson, 1998), and dry forest in Tikal, Guatemala (Cant, 1986). The black spider monkey (A. paniscus) has been observed in two similar high wet terra-firme forests from the Guianan plateau, in Raleighvalen-Voltzberg, Suriname (Mittermeier, 1978) and Nouragues, French Guiana (Youlatos, 2002). Finally, the white-bellied spider monkey (A. belzebuth belzebuth) has been studied in a wet terra firme forest in Yasuni National Park, Ecuador (Cant et al., 2001, 2003; D. Youlatos, J. G. H. Cant and D. M. Rose, unpublished data). Below I compare the quantitative aspects of the locomotion and postures of the different species across the different habitats, aiming to set a background for further discussions concerning phylogenetic or habitat structural aspects.

All species of Ateles appear to employ relatively high rates of quadrupedal activities. Quadrupedal walk and run varies from around 21%–25% for
Table 7.2 Summary of percentages of postural categories in positional studies of species of Ateles

<table>
<thead>
<tr>
<th>Site</th>
<th>A. geoffroyi</th>
<th>A. paniscus</th>
<th>A. belzebuth</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rain forest</td>
<td>Panama</td>
<td>Guatemala</td>
<td>Panama</td>
</tr>
<tr>
<td>Sampling post</td>
<td>wet bout</td>
<td>dry 30-sec</td>
<td>wet bout</td>
</tr>
<tr>
<td>Sit</td>
<td>33.8%</td>
<td>45.0%</td>
<td>55.10%</td>
</tr>
<tr>
<td>Stand</td>
<td>5.5%</td>
<td>3.0%</td>
<td>5.62%</td>
</tr>
<tr>
<td>Suspended</td>
<td>53.7%</td>
<td>52.0%</td>
<td>30.71%</td>
</tr>
<tr>
<td>Tail-only hang</td>
<td>(3.5%)</td>
<td>20.0%</td>
<td>7.44%</td>
</tr>
<tr>
<td>Tail–hindlimbs</td>
<td>2.59%</td>
<td>11.3%</td>
<td>16.0%</td>
</tr>
<tr>
<td>Tripod</td>
<td>21.0%</td>
<td>1.58%</td>
<td>13.1%</td>
</tr>
<tr>
<td>Tail–forelimbs</td>
<td>11.0%</td>
<td>20.11%</td>
<td>8.4%</td>
</tr>
</tbody>
</table>


A. geoffroyi in Panama, A. paniscus in both French Guiana and Suriname, and A. belzebuth in Ecuador, up to 50% for A. geoffroyi in Guatemala, where vertical quadrupedal climb is included in the quadrupedal category (Cant, 1986). Proportions of vertical climbing for A. geoffroyi in Panama range between 9% and 16% (Mittermeier, 1978; Fontaine, 1990). Comparable rates are observed in A. belzebuth (12.5%; Cant et al., 2001) and A. paniscus in Suriname (9%; Mittermeier, 1978), but yet much lower for the latter species in French Guiana (2.3%; Youlatos, 2002).

Pronograde, ascending and descending clamber also varies significantly across species and forests. Ateles belzebuth in Ecuador and A. paniscus in French Guiana engage in quite high proportions (28.2% and 25.8% respectively; Cant et al., 2001; Youlatos, 2002), and a slightly lower rate (20%) is encountered for A. geoffroyi in Guatemala, if the transitional mode is included in this category (Cant, 1986). However, proportions stay as low as 8–9% in both Panama and Suriname (Mittermeier, 1978; Fontaine, 1990). Bipedalism is quite uncommon, scoring particularly low in Panama, Suriname, and Ecuador (0.6–0.8%; Mittermeier, 1978; Cant et al., 2001) to 1.7% in French Guiana (Youlatos, 2002) and 2.23% in Panama (Fontaine, 1990).

Leap and drop are used commonly by A. geoffroyi in Panama (Table 7.1; Mittermeier, 1978; Fontaine, 1990), while very rarely in Guatemala (Cant, 1986). Both A. paniscus and A. belzebuth show consistently lower rates (2.3–4.2%) in all forests (Table 7.1; Mittermeier, 1978; Cant et al., 2001; Youlatos,
Table 7.3 Tail–limb(s) hang/tail-only hang ratio (TL/T), tail–arm brachiation/forelimb swing ratio (TAB/FSW), and leap/drop ratio (L/D) across studies of positional behavior of Ateles

<table>
<thead>
<tr>
<th></th>
<th>TL/T</th>
<th>TAB/FSW</th>
<th>L/D</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ateles geoffroyi</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Panama1</td>
<td>14.15</td>
<td>1.44</td>
<td>–</td>
</tr>
<tr>
<td>Guatemala2</td>
<td>1.60</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Panama3</td>
<td>3.34</td>
<td>16.67</td>
<td>4.68</td>
</tr>
<tr>
<td>Costa Rica4</td>
<td>1.44</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ateles paniscus</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Suriname1</td>
<td>7.93</td>
<td>1.49</td>
<td>–</td>
</tr>
<tr>
<td>French Guiana5</td>
<td>1.94</td>
<td>10.00</td>
<td>6.5</td>
</tr>
<tr>
<td>Ateles belzebuth</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ecuador6,7,8</td>
<td>2.19</td>
<td>4.17</td>
<td>6.8</td>
</tr>
</tbody>
</table>

1: Mittermeier (1978); 2: Cant (1986); 3: Fontaine (1990); 4: Bergeson (1998); 5: Youlatos (2002); 6: Cant et al. (2001); 7: Cant et al. (2003); 8: D. Youlatos, J. G. H. Cant and D. M. Rose, unpublished data.

2002). These proportions, however, mask the use of active (leap and jump) versus passive (drop) airborne locomotion, and leaping dominates and is used over five times more than dropping in all studies where detailed data are available (Table 7.3; Fontaine, 1990; Cant et al., 2001; Youlatos, 2002).

Suspensory locomotion is employed in similar proportions in A. geoffroyi and A. belzebuth (23–26%; Mittermeier, 1978; Cant, 1986; Fontaine, 1990; Cant et al., 2001, 2003). In contrast, A. paniscus appears to be the most suspensory species with rates up to 38.6% in Suriname and 35.2% in French Guiana. In addition, significant differences exist in the ratio of use between tail–arm brachiation and forelimb swinging across species and sites. Brachiation is used over 10 times more than forelimb swing in Panama (Fontaine, 1990) and French Guiana (Youlatos, 2002; Table 7.3) or can be more equally shared in Panama and Suriname (Mittermeier, 1978). In A. belzebuth, the same ratio is intermediate (Table 7.3), and bouts of both modes are mainly complete or full stride (Cant et al., 2003). Ateles belzebuth bridges gaps extensively (12.5%), while lower proportions are encountered in A. paniscus, and even lower in A. geoffroyi (Table 7.1).

In terms of postural behavior, only feeding postures that are active and necessary for forage procurement are considered here, Fontaine’s (1990) study being an exception by not including behavioral contexts. In A. geoffroyi, sitting is by far the most dominant posture, and it may or may not involve the...
ischia, and rates of use may be as moderate as 25.7% in Costa Rica (Berge-son, 1998) to as high as 55.1% in Panama (Fontaine, 1990). Ateles belzebuth also show moderate rates (26.1%) in Ecuador (D. Youlatos, J. G. H. Cant and D. M. Rose, unpublished data) whereas sitting was particularly frequent for A. paniscus in French Guiana and especially in Suriname (Table 7.2; Mittermeier, 1978; Youlatos, 2002). Stand also shows variable rates across species and sites, scoring high in Ecuador, Costa Rica and Suriname (16.3%, 12.6%, and 13.1% respectively; Mittermeier, 1978; Bergeson, 1998; D. Youlatos, J. G. H. Cant and D. M. Rose, unpublished data) and particularly low in Panama, French Guiana and Guatemala (Table 7.2).

On the other hand, rates of suspended postures are variable across sites for the different species. Thus, A. geoffroyi show high rates in Panama (30.7%; Fontaine, 1990) and Costa Rica (33.3%; Bergeson, 1998), and especially high ones in Panama (53.7%; Mittermeier, 1978) and Guatemala (52%; Cant, 1986). Similarly, particularly high rates are also exhibited by A. paniscus in both French Guiana (55.4%; Youlatos, 2002) and Suriname (41.2%; Mittermeier, 1978), and A. belzebuth in Ecuador (55.5%; D. Youlatos, J. G. H. Cant and D. M. Rose, unpublished data).

In a finer analysis of suspensory postural behavior, tail-only suspension (7.44%; Fontaine, 1990) or one-limb hanging (6.6%; Mittermeier, 1978) accounts for a small proportion of the suspensory profile of A. geoffroyi in Panama (Table 7.2). Low rates are also encountered in A. paniscus in Suriname (Mittermeier, 1978). In contrast, tail-only hang represents 20% of total postural behavior of A. geoffroyi in Guatemala (Cant, 1986), and reaches a total of 41% of the suspensory feeding behavior in Costa Rica (Bergeson, 1998). Similarly, A. paniscus in French Guiana (18.8% of all postures), and A. belzebuth in Ecuador (31.3% of suspensory subsample) exhibit comparably high rates of tail-only suspension (Table 7.2; Youlatos, 2002; D. Youlatos, J. G. H. Cant and D. M. Rose, unpublished data).

In A. geoffroyi, tail–hindlimbs-assisted suspension appears to be very common in Costa Rica (13.1%) and Guatemala (21%), defined as tripod and inverted bipedal respectively (Cant, 1986; Bergeson, 1998). In a similar manner, tripod scores significant rates (16.1%) in A. belzebuth in Ecuador, and when added to the particularly high rates of tail–hindlimbs-assisted hanging (24.4%) the total use of the hindlimbs and the tail is predominant among suspensory postural behavior. On the other hand, in French Guiana, rates of tripod are low (7.9%) but proportions of tail–hindlimbs-assisted suspension can reach high rates, should the former be added to the tail–hindlimb(s) hang category (Table 7.2; Youlatos, 2002).

The involvement of forelimbs under tension in suspensory postural behavior is relatively consistent. In A. geoffroyi, rates range from 11% in Guatemala to
16% in Panama, while data from Panama and Costa Rica (Mittermeier, 1978; Bergeson, 1998) are hard to decipher and it is therefore difficult to gauge forelimb use under suspension. *Ateles paniscus*, in French Guiana, show comparable rates when both tail–forelimb and tail–forelimb–hindlimb hang are included (total of 13%; Youlatos, 2002) that are similar to *A. belzebuth* from Ecuador (21.5% of suspensory subsample; D. Youlatos, J. G. H. Cant and D. M. Rose, unpublished data). Comparing the ratios of tail-only to tail–limb hanging across species, it is evident that most studies show that the latter is used from 1.5 to 2.2 times more than the former (Table 7.3). This shows a more or less equal use of these suspensory modes and provides evidence for the important role of the prehensile tail supporting whole body weight during feeding suspensory behavior. Particularly high ratios are found in Mittermeier’s (1978) study, but this may be due to his definitional differences (Table 7.3).

These quantitative data on the positional behavior of the three species of *Ateles* can only be considered as indicative for each species and the genus in general. The use of different methods of data collection during different study seasons and periods in addition to different definitional systems of positional modes may render intra- and interspecific analyses and comparisons difficult. Moreover, variability in rates of use of different locomotor modes may also be related to the rapid and fluid locomotion of *Ateles*, occurring within and across trees, making them difficult to observe in detail. On the other hand, the relative consistency in rates of supported versus suspended postural behavior may be related to the fact that these postures occur for longer periods within a single tree and on a specific fruit patch. They are therefore easier to observe and sample than some other behaviors. In all cases, a gross profile of the locomotion and feeding postural behavior of the genus can be outlined.

Spider monkeys extensively employ suspensory forelimb dominated locomotion that mainly involves tail–arm brachiation and forelimb swing in variable rates. Pronograde quadrupedal activities, involving either walk/run on single substrates or clamber across multiple ones, also represent a major component of their locomotor profile. Vertical climb is used variably but in relatively notable proportions. Lastly, active and passive airborne locomotion appears to play a minor role in the overall repertoire of *Ateles* spp. During feeding, suspensory and nonsuspensory postures appear to be shared relatively equally. Sitting is the dominant supported posture. The rates of suspensory feeding are particularly high and outrank all other nonhominoid anthropoids. In contrast to hominoid suspensory feeding, however, the use of the tail by *Ateles* appears to be primordial during suspended feeding. This is depicted by the notably high rates of tail-only hanging in most species, but also in the constant use of the tail in all below-substrate postures.
These observations support the fact that *Ateles* is by far the most suspensory of all atelines and of all platyrrhines. Among atelines, the positional behavior of *Lagothrix* (woolly monkeys) appears to approximate that of *Ateles*, containing a diversity of forelimb and hindlimb suspensory modes in relatively high proportions but is still dominated by pronograde above support behavior (Defler, 1999; Cant *et al.*, 2001; 2003). Howler monkeys (*Alouatta* spp.) depend mainly on pronograde modes during locomotion, albeit showing respectable rates of tail–hindlimb suspensory feeding (Fleagle and Mittermeier, 1980; Schönybarra, 1984; Cant, 1986; Schönybarra and Schö, 1987; Bicca Marques and Calegaro Marques, 1995; Bergeson, 1998; Youlatos, 1998). The morphology of the postcranial skeleton of *Brachyteles*, coupled with limited postural data, advocate behavioral similarities with *Ateles* that remain to be examined in the field (Erikson, 1963; Nishimura *et al.*, 1988; Jones, 2004).

Although the above studies provide a general positional profile for *Ateles* that differentiates it from the rest of the atelines, a finer analysis suggests several intra- and interspecific differences. As noted above, these differences may result from diverse methodological approaches adopted during the different studies. However, they may be also related to the utilization of specific structural features of the different habitats due to intrinsic forest architecture or seasonal exploitation of different food sources, or to phylogenetic constraints.

In terms of phylogeny, it appears that *A. paniscus* is the most suspensory species employing high rates of both suspensory locomotion and bridging, as well as suspensory feeding, with *A. belzebuth* being intermediate, with relatively intermediate rates of suspensory locomotion but high rates of suspensory feeding. The same studies indicate that *A. geoffroyi* may be the least suspensory species, showing the lowest rates of suspensory locomotion coupled with variable rates of suspensory feeding. It also appears that the latter species may be the most terrestrial one, as it exhibits the higher rates of terrestriality, although multiple reasons may account for this (Campbell *et al.*, 2005).

**Locomotion, postures, and canopy use in *Ateles***

Locomotion and postures are developed through a constant interaction with the physical structure of the surrounding environment of the tropical forest canopy. Locomotion inflicts constraints as animals are called to cope with continuously emerging problems within time and space as they travel within the canopy. The problems may be multiple and require a diversity of solutions to help the animal get through the canopy and attain food sources and mates (Cant, 1992). On the other hand a different set of somewhat more “static” problems emerge during
D. Youlatos

feeding. Although these problems may be more demanding to solve, there is likely a larger diversity of alternatives of appropriate behaviors available to the animal. The above studies of the positional behavior of *Ateles* have revealed a diversity of both locomotor and postural behavior. As discussed above some of the differences among the different species of *Ateles* may reside in phylogenetic constraints, but the study of the same species in different habitats may provide evidence for a differential use of structural differences in relation to anatomical design.

The main habitat that *Ateles* exploit is the higher levels of the canopy of tropical forests (Mittermeier and Roosmalen, 1981; Roosmalen, 1985; Youlatos, 2002). These parts of the forest are characterized by intertwining tree crowns that are mainly composed of small, flexible branches. This more or less continuous structure is however interrupted by the presence of vertically and horizontally distributed gaps of variable sizes between adjacent trees. In addition, emergent crowns that are disconnected from, and communicate with, the rest of the canopy via large vertical or subvertical substrates and wide gaps are also a component of this part of the forest. *Ateles* need to deal with these features of the canopy in order to find patches of ripe fruit trees and to gain access to fruit- or flush leaf-bearing substrates in the tree crown peripheries (Grand, 1972; 1984; Cant, 1992). In effect, the diversity of locomotion and postures that they exhibit, are the behavioral means that enable them to deal with all aspects of habitat structure that may facilitate or impede the access to valuable food sources.

Initially, monkeys need to obtain access to these fruit trees that are randomly dispersed in time and space in the canopy of the tropical forest. Spider monkeys are ripe fruit specialists, obliged to look for trees that bear fruit at the right moment (Roosmalen, 1985; Symington, 1988b; Cant, 1990; Strier, 1992; Guillotin *et al*., 1994; Simmen and Sabatier, 1996; Nunes, 1998; Iwanaga and Ferrari, 2001; Pozo, 2001; Dew, 2005; Wallace, 2005; Di Fiore and Campbell, 2007). Recent research has demonstrated that they appear to use a Levy walk pattern of traveling within their home ranges (Ramos-Fernández *et al*., 2004). In this way, they show spatial scale invariance in the length of constituent steps and temporal invariance in the duration of intervals between steps. This appears to contribute more to the exploitation of these random scarce food sources that are far from uniform in their distribution and show a temporal and spatial variation. Levy walking aids in visiting more new sites and revisiting less previously visited sites. This pattern is strongly related to fruiting tree distribution that appears to follow a more or less fractal manner. Long infrequent steps could be those between known patches and shorter more frequent steps would be given while foraging within a patch. Avoiding revisiting previously visited fruit patches and/or revisiting them after appropriately long periods of time enhances
the possibility of finding them bearing more ripe fruit (Ramos-Fernández et al., 2004).

This strategy would imply fast traveling within the canopy, the shortening of pathway distances, and a variety of locomotor modes that could provide safe crossing of canopy gaps (Cant, 1992). Spider monkeys do appear to travel fast in the canopy in a similar but probably less acrobatic way than gibbons do (Cant, 1992). I have reported that travel speeds for brachiation bouts were significantly higher than those for quadrupedal walk (1.72 m/s vs. 0.84 m/s) in French Guiana (Youlatos, 1994). In addition, Cant (1986) found that spider monkeys traveled faster than howlers in all contexts in Guatemala. Brachiation is a form of locomotion that is energetically maximizing but may compensate body displacement in the forest canopy by enabling its performers to travel faster and, perhaps, to shorten pathways within and across tree crowns (Parsons and Taylor, 1977). It is thus very likely, that the consistently high proportions of tail-arm brachiation of spider monkeys do contribute to faster traveling within and across tree crowns. Moreover, suspensory sensu lato locomotor modes (i.e. tail-arm brachiation, forelimb swing, clambering, bridging) would help relatively large-bodied animals to move quite safely on slender flexible supports (Grand, 1984). Within a single crown, these modes would allow for rapid movements across supports avoiding zigzags that follow the more stable main branch forks in the central part of the crown (Grand, 1984). This helps reduce certain pathways within the same tree or across trees within intertwined crowns that bear no gaps.

On the other hand, crossing gaps between trees appears to be a very important determinant of shortening pathways, and can be extremely important for primates with long day ranges such as spider monkeys (Cant, 1992). Although smaller arboreal mammals tend to leap in order to traverse gaps, larger ones use more cautious and deliberate ways such as bridging (Youlatos, 1993), tree sways or vine crossings (Cant, 1992). This may account for the relatively low rates of leaping behavior generally observed in Ateles. However, studies have shown that, at least for A. geoffroyi, leaping is quite common in Panama and relatively infrequent in Guatemala, further accompanied by low rates of quadrupedalism in the former forest versus high ones in latter (Mittermeier, 1978; Cant, 1986; Fontaine, 1990). Such observations may imply differences in habitat structure between the two forests. The dry forests of Guatemala may be more discontinuous with larger canopy gaps and a higher frequency of relatively “isolated” trees. This would eventually compel spider monkeys to use less leaping, as gaps would be larger and almost impossible to cross with such means, and impose a higher use of quadrupedal or suspensory modes to travel within single trees in order to obtain access to inter-crown passages that are negotiable for the animals. Thus, spider monkeys appear to heavily employ bridging and suspensory
modes such as tail-arm brachiation in order to traverse gaps (Bergeson, 1996; Cant et al., 2001). However, it is not clear as to how and under what conditions certain modes are opted or avoided. Could this actually provide path shortening or fast crossing within the canopy? This is hard to answer, but it may very likely help reduce pathways within and across trees in order to give spider monkeys a selective advantage for reaching more fruit trees within their large home ranges. To date, no study has specifically explored succession and shifting of locomotor modes in relation to habitat structure availability, in order to assess alternative solutions that appear to allow the animals to avoid time-and energy-consuming detours.

In effect, there are no detailed data on the different modes that spider monkeys employ during traveling within and across canopy trees in order to gain access to the desired fruit sources. However, it would be interesting to determine whether there are differences in both the frequency as well as sequence of locomotor modes employed during these differential approaches of known and unknown fruit patches. This would demand a large and short scale analysis of the sequence of modes so that a pattern could arise of the different solutions that spider monkeys use in respect with the structure of the different trees. This approach would help in the investigation of locomotor behavior in a wider adaptive context. The sequence of modes could elucidate the range of eventual selections that enable spider monkeys to cope with the structural diversity of their environment while also acknowledging the adaptive significance of foraging patterns from the locomotion-postcranium complex point of view (Cant, 1992). Such a study should cover both selection at the broader scale (i.e. locomotion across trees and overall traveling patterns) as well as at the finer scale (i.e. locomotion within a single tree), thus allowing a test of the proximate causes of mode selection. Would spider monkeys select for speed and quicker displacement across the canopy? Would they prefer or avoid large vertical structures that provide direct and rapid changes of vertical location in the canopy? Could all these provide shortening of pathway distances? How are gaps traversed, and is there any relationship between the 3-dimensional structure of the gap and locomotor options selected? These problems, although thoroughly described and partially tackled by Cant (1992) are far from having a tangible answer. Thus far, most studies focus on anatomical correlates, rather than providing answers to the questions I have outlined.

In addition, it is well established that spider monkey males have larger home ranges and travel further per day than females (van Roosmalen, 1985; Symington, 1988a; Strier, 1992; Nunes, 1995; Shimooka, 2005). It would thus be interesting to test whether there are differences in the frequencies and sequences of locomotor modes between males and females. Because spider
Locomotion and positional behavior

Monkeys are monomorphic in body size (Di Fiore and Campbell, 2007), eventual sex differences could be related to differential canopy use rather than body size differences. A similar comparative study could shed light on the modes that are actually related to path shortening or faster traveling within the forest canopy.

Another major problem that arboreal dwellers face is the way that food is actually acquired, manipulated, and consumed (Cant, 1992). As ripe fruit specialists and flush leaf consumers, spider monkeys are compelled to negotiate the terminal branches of tree crown peripheries. Such a microhabitat involves small, slender and fragile substrates, whereupon relatively large-bodied arboreal animals face difficulty in maintaining equilibrium and face a high risk of toppling over and falling. In this context, below-branch suspensory patterns or above-branch distribution of body weight through cautious body displacement or dynamic maintenance may provide substantial solutions to overcome this problem (Cartmill, 1985; Cant, 1987; Bergeson, 1998; Dunbar and Badam, 2000).

Such modes appear to be used at quite high rates during feeding activities in most primate species and may provide quicker and safer access to food-bearing substrates, enabling them to explore, detect, locate, approach, acquire and ingest the desired food items (Grand, 1972; Cant, 1992). In spider monkeys this is further achieved by the increased use of the prehensile tail in both suspended and supported locomotor and postural modes offering substantial support during both foraging movements and food acquisition. Sarmiento (1995) asserted that the deliberate climbing (= clambering) heritage of atelines (and hylobatids) evolved in more suspensory habits mainly to solve fruit-eating problems. This may hold true for siamangs in Malaysia (Fleagle, 1976) but data for the atelines do not support similar assumptions (Bergeson, 1998; Youlatos, 2002). The use of high rates of suspended positional modes during both fruit and flush leaf acquisition in Ateles most likely supports the idea that similar behaviors are associated with the characteristic energy-maximizing strategy that the protoclineae must have adopted (Jones, 2004). However, postural data for A. paniscus in similar forests reveal strong differences in rates of sit, stand, and suspensory postural behavior (Mittermeier, 1978; Youlatos, 2002). This may be related to differences in food sources acquired during different seasons. A similar pattern has been observed in Alouatta and has been related to differences in microhabitat and temporal and spatial distribution of food sources (Youlatos, 1998). These observations denote the importance of structural differences of habitat features on the postural behavior of Ateles, providing evidence for further research focusing on the interaction between postural behavior and microhabitat structure, as well as the options of positional modes selected within such contexts.
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References


Locomotion and positional behavior


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