

Pendular Motion in the Brachiation of Captive *Lagothrix* and *Ateles*

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Pendular motion during brachiation of captive *Lagothrix lagothricha lugens* and *Ateles fusciceps robustus* was analyzed to demonstrate similarities, and differences, between these two closely related large bodied atelines. This is the first captive study of the kinematics of brachiation in *Lagothrix*. Videorecordings of one adult male of each species were made in a specially designed cage constructed at the DuMond Conservancy/Monkey Jungle, Miami, FL. Java software (Jandel Scientific Inc., San Rafael, CA) was used for frame-by-frame kinematic analysis of individual strides/steps. Results demonstrate that the sequence of hand and tail contacts differ significantly between the two species with *Lagothrix* using a new tail hold with every hand hold, while *Ateles* generally utilizes a new tail hold with only every other hand hold. Stride length and stride frequency, even after adjusting for limb length, also differ significantly between the two species. *Lagothrix* brachiation utilizes short, choppy strides with quick hand holds, while *Ateles* uses long, fluid strides with longer hand holds. During brachiation not only is *Lagothrix*'s body significantly less horizontal than that of *Ateles* but also, within *Ateles*, there are significant differences between steps depending on tail use. Because of the unique nature of tail use in *Ateles*, many aspects of body positioning in *Lagothrix* more closely resemble *Ateles* steps without a simultaneous tail hold rather than those with one. Overall pendulum length in *Lagothrix* is shorter than in *Ateles*. Tail use in *Ateles* has a significant effect on maximum pendulum length during a step. Although neither species achieves the extreme pendulum effect and long period of free-flight of hylobatids in fast ricochet brachiation, in captivity both consistently demonstrate effective brachiation with brief periods of free-flight

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and pendular motion. Morphological similarities between ateline brachiators and hylobatids are fewer and less pronounced in *Lagothrix* than in *Ateles*. This study demonstrates that *Lagothrix* brachiation is also less hylobatid-like than that of *Ateles*. *Am. J. Primatol.* 48:263–281, 1999. © 1999 Wiley-Liss, Inc.

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INTRODUCTION

Primates vary widely in their positional behavior and in the morphology that underlies it. These various morpho-behavioral specializations represent adaptations that allow primates to exploit a variety of terrestrial and arboreal habitats. They are therefore crucial aspects of the ecological relationships of any primate taxon. Similarly, major evolutionary changes within primate lineages have generally been associated with morphological change in the postcranial skeleton and concomitant change in deduced positional behavior [see, e.g., Fleagle, 1999].

Among anthropoid primates, the atelines (*Ateles*, *Brachyteles*, *Lagothrix*, and *Alouatta*) provide a good example of variation in functional morphology and positional behavior among a group of closely related taxa. While they share many components of their positional repertoires, the incidence and style of performance of the elements of the repertoire vary. This is particularly evident in suspensory behavior, which is most emphasized in *Ateles* and least emphasized in *Alouatta*. Suspensory behavior is also an important component of the positional repertoire of extant non-human hominoids. It may have evolved independently several times in anthropoid taxa, including a number of fossil catarrhine taxa [Rose, 1997; Larson, 1998]. Thus some Miocene catarrhines, such as *Pliopithecus* and *Dendropithecus*, share a number of, especially, forelimb features with atelines [Rose, 1993b, 1996, 1997]. However, the exact combination of features does not closely match those of any particular extant ateline genus. Also, it is likely that the Miocene taxa were either short-tailed or tail-less [Ankel, 1965; Ward et al., 1991]. Nevertheless, extant atelines constitute the closest living models for some aspects of the morphology and deduced positional behavior of the fossil taxa.

A detailed knowledge of the links among structure, function, and behavior among extant atelines is necessary in order to understand the variations among their positional behaviors and in order to fully utilize them as partial models for understanding the positional adaptations of fossil taxa. The results presented here form one part of an ongoing comprehensive study of atelines that includes field observations of positional behavior in natural habitats, kinematic analysis of positional behavior under controlled conditions, and quantitative study of musculoskeletal anatomy. In this study kinematic analysis forms a crucial link between the morphological and behavioral investigations. It allows both morphological detail and elicited natural behaviors to be interpreted in quantitative functional terms.

Bimanual suspensory locomotion in *Lagothrix* (the woolly monkey) and *Ateles* (the spider monkey) has been variously labeled as brachiation, semibrachiation, and arm-swinging [e.g., Ashton & Oxnard, 1964; Napier, 1963; Napier & Napier, 1967; Erikson, 1963; Andrews & Groves, 1976; Hollih, 1984]. Regardless of the precise definition of brachiation, it is clear that bimanual progression (arm-swinging) beneath a support is a common locomotor pattern among hylobatids and some atelines [e.g., Jenkins et al., 1978; Jungers & Stern, 1981]. Field studies, which have helped to define the locomotor and postural repertoire of *Ateles*, have concluded that brachiation is an important part of their repertoire in the wild

[e.g., Mittermeier & Fleagle, 1976; Mittermeier, 1978; Cant, 1986; Cant et al., 1996]. This form of locomotion has also been studied in a variety of ways in the laboratory where each study has been limited to the role of a specific anatomical region [e.g., Jenkins, 1981; Jenkins et al., 1978; Stern et al., 1980; Jungers & Stern, 1981; Turnquist, 1975]. Prior to recent work by Cant et al. [1996], information on *Lagothrix* in the wild was extremely sparse and included only passing references to its locomotion. Similarly, published data on *Lagothrix* locomotion in the laboratory is limited to rare comparative studies [e.g., Stern et al., 1980]. Thus, although the problem of the kinematics and kinetics of brachiation in prehensile tailed atelines has been touched upon by various researchers, to date there is no comprehensive study of this form of locomotion in large bodied atelines. The current paper is intended to partially fill this gap. This is the first detailed analysis of *Lagothrix* brachiation in captivity as well as a comparison between its brachiation and that of its closest relative, *Ateles*. The data presented here delineate both similarities and differences in the brachiation potential and pendular motion of these large bodied prehensile tailed atelines in captivity.

A number of studies have noted numerous morphological similarities between ateline brachiators (particularly *Ateles*) and hylobatids [e.g., Erikson, 1963; Jenkins, 1981; Larson, 1993; Lewis, 1971; Rose 1993a; Sarmiento, 1985]. These observations have been confirmed and extended during this ongoing comprehensive study and will be presented in detail elsewhere. Similarities between ateline brachiators and hylobatids are strongest in *Ateles*, although its morphological specializations are rarely as extreme as in hylobatids. Features of similarity include trunk shape, the relative elongation of the forelimb, the morphology of the shoulder girdle, and some aspects of the articulations in the shoulder, elbow, forearm, and carpus. Similarities are fewer and even less pronounced in *Lagothrix*. Indeed, in many features of its shoulder girdle and scapulohumeral joint, *Lagothrix* more resembles predominantly quadrupedal anthropoids than it does hylobatids and *Ateles*. These variations in functional morphology are matched by comparable differences in positional behavior. As reported by Cant et al. [1996], both *Ateles* and *Lagothrix* have a more varied locomotor repertoire than that of hylobatids. Suspensory activities account for approximately 23% of locomotor activities in *Ateles* and 12% in *Lagothrix*. As well as suspensory activities being less emphasized in its locomotor repertoire, *Lagothrix* performs less multi-step suspensory activities and more activities that are briefer in duration. The kinematic patterns of brachiation presented in this paper can thus be related to previously observed anatomical and behavioral differences among *Lagothrix*, *Ateles*, and other brachiators.

MATERIALS AND METHODS

The kinematics of brachiation in *Lagothrix lagothricha lugens* and *Ateles fusciceps robustus* were analyzed from videotapes of one adult male of each species. Although the locomotion of only one individual of each species was sampled, we are confident that their locomotion is typical of these species. The *Ateles fusciceps* individual was a 10-year old male who weighed 8.2 kg and the *Lagothrix lagothricha* was a 6-year old male who weighed 8.8 kg. Both exhibited complete adult dentition with occlusal wear. The weight and body proportions of each animal were measured under chemical restraint (Ketamine HCl 12 mg/kg intramuscularly) and found to be within published ranges for their genera/species [Napier & Napier, 1967; Fleagle, 1999]. Each individual receives a controlled diet and neither exhibited noticeable obesity or suffered from any obvious defor-

mities. Radiographs and passive movement of the joints of the limbs and tail did not indicate any limitation of joint mobility in either animal. Both animals are normally housed with sufficient space and appropriate cage furniture to allow them a full range of locomotor activities. Of even more importance, however, is that the locomotor behavior of each individual, and the inter-individual differences, correspond closely to the behavior we have observed in natural populations of these species [Cant et al., 1996]. The basic movement patterns for *Ateles* observed in this study are similar to those of previous captive observations [Jenkins et al, 1978; Jungers & Stern, 1981; Turnquist, 1975]. During the course of the study, both animals were housed at the DuMond Conservancy/Monkey Jungle in Miami, Florida.

All videotapes were recorded in a specially designed videocage, which was constructed at the DuMond Conservancy by this study's principal investigators (J.E.T., M.D.R., and J.G.H.C.). The 7.8 m × 1.7 m × 2.1 m videocage, constructed of galvanized pipe and chainlink with a moveable back wall, is raised 46 cm off the ground. To ensure an unobstructed view for videorecording, the middle section chainlink fence in the front wall and the ceiling of the videocage has been replaced by 2.5 m panels of 6.4 mm Lexan (a polycarbonate trademark, Sheffield Plastics, Sheffield, MA). A similar Lexan panel replaced the chainlink at one end of the videocage. Thus videorecording in all three planes is unobstructed. To facilitate the transfer of unrestrained animals to and from the videorecording cage, two 2.1 m × 2.1 m × 2.4 m holding cages were also constructed as well as a 4.6 m diameter × 6.1 m high modified corncrib homecage for *Lagothrix*. All components are connected by chainlink tunnels and double security doors. Brachiation sequences were videorecorded on a 6.4 m section of 3.5 cm galvanized steel pipe suspended on galvanized steel brackets 30 cm below the ceiling.

During videorecording, video cameras were positioned 7.6 m from the brachiation pole in the lateral view and 1.2 m from the brachiation pole in the overhead view. In the frontal view the animal was 4.5–7.6 m from the camera depending on its movement toward, or away from, the camera. To minimize parallax distortion the macrozoom lenses (8:80, ratio 1–1.4) on the lateral and frontal cameras were zoomed in on the subjects [as per method of Plagenhoef, 1968, 1979; Winter, 1990]. A shutter speed of 1/1,000 of a second was used for all videorecordings in Super-VHS format at 60 fields (30 frames) per second.

Frame-by-frame analysis of videorecordings utilized a Panasonic AG6300 frame-by-frame videorecorder, a Sony Trinitron PVM1341 monitor, and a Gateway 2000 computer in conjunction with Java software (Jandel Scientific, Inc., San Rafael, CA) in the Morphometrics Laboratory at Duke University. Sequences were viewed frame-by-frame and critical events within the stride were analyzed kinematically.

The data presented here is the result of analysis of images recorded from the lateral view with supplementary information derived from frontal view recordings. Thirty strides (period between consecutive handholds of the same hand) of *Lagothrix* and eighteen strides of *Ateles* were analyzed for temporal data. The movement of each appendage during a single stride is subdivided into a support phase (when the extremity is in contact with the support) and a swing phase (when the extremity is not in contact with the support, i.e., when it is swinging forward towards the next point of contact). Twenty steps (period between handholds of contralateral hands) of each species were analyzed for kinematic data. During *Ateles* brachiation, the two steps which make up a single stride are generally asymmetrical and thus steps, not strides, were used for all kinematic analysis. To minimize possible effects of fatigue, strides (steps) from the begin-

ning, middle, and end of videorecording sessions were randomly selected for analysis. Only sequences with continuous motion across the field and no marked acceleration or deceleration were analyzed. Measurements included both linear distance and angles (in degrees). The direction in which the arc was swung in angular measurements indicates the path of motion away from the 0° reference line. The critical events analyzed for each stride sequence were: touchdown (grasping of the support), midsupport, and liftoff (release of the support) of each of the three appendages (left forelimb, right forelimb, and tail).

For each critical event, the following variables were measured on the lateral view recordings (Fig. 1A,B): linear distances (Fig. 1A) of the positions of the shoulder and hip below the support were measured as the shortest distance between the center of the brachiation pole and the location of the joint along the body axis (a line drawn between vertebrae C7 and the hip). X,Y coordinate data were collected on the same two points. Angular measurements (Fig. 1B) were made of the degree of flexion at the shoulder, elbow, hip, and knee joints. In all cases the arc of the angle was swung towards the flexor surface and measurements of the shoulder and hip utilized the body axis as the 0° reference line. Two angular measurements of the tail were collected to quantify its position. One measured the dorsal (hyperextension) angle between the body axis and the axis of the thickest portion of the proximal (base of) tail. The second measured the dorsal angle between the axis of the thickest portion of proximal tail and the axis of the midtail region (not including the tail pad). A final angular measurement measured the angle between the dorsum of the body axis and the horizontal brachiation pole. Together the linear and angular measurements quantify not only the position of the body in space (Fig. 1A) but also the intersegmental relationships between the body, limbs, and tail that contribute to this positioning (Fig. 1B).

Calculated variables include speed, stride frequency, duty factor, adjusted stride length and frequency, and pendulum length. Speed is distance divided by time, i.e., m/sec. Stride frequency is the number of strides per sec. To calculate duty factor, support time is divided by stride time, which results in the percentage of time that each hand is in contact with the support during a stride. Ad-

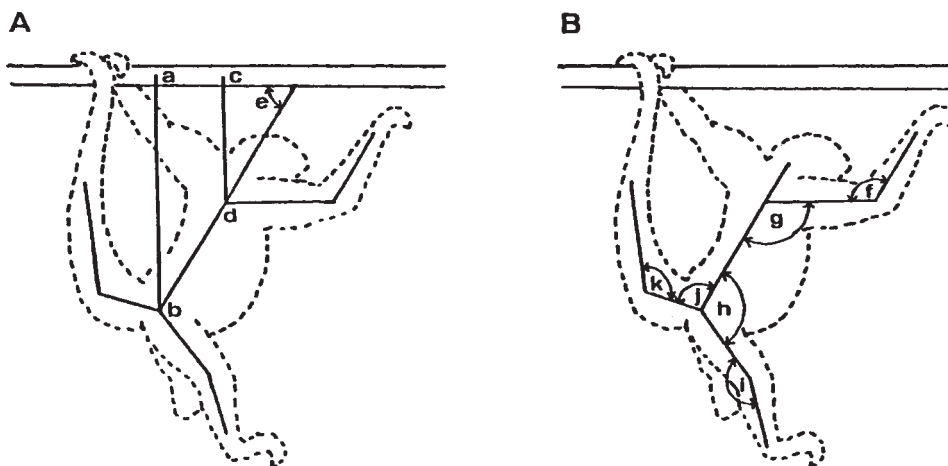


Fig. 1. Measured variables. **A:** Distance of hip (a,b) or shoulder (c,d) below center of brachiation pole; x,y coordinates of hip (b) and shoulder (d); angle of body axis below brachiation pole (e). **B:** Angle of elbow (f), shoulder (g), hip (h), knee (i), proximal tail to body axis (j), and proximal tail to midtail (k).

justed stride length and frequency take into account differences in body size by dividing either stride length or stride frequency by forelimb length, i.e., the combined length of the brachium and antebrachium. Pendulum length is similarly adjusted to body size by dividing the distance between the center of mass and the brachiation pole by the combined length of the forelimb and body.

All statistics were computed with the program SAS-PC on a Gateway 2000 personal computer. Kinematic values across subjects (species) were compared in three ways. First, a G-test was used to statistically compare the frequency of behavior (i.e., a tail hold to accompany every hand hold) observed in the two species [Sokal & Rohlf, 1981]. This statistical comparison determined if, in fact, there were significant differences in the frequency of tail contact between the species. Second, the means and the average minimum and maximum values for all kinematic variables were compared using the methods of Schmitt [1994, 1995, 1998]. This approach was developed to compare the kinematic patterns of subjects regardless of the timing of the specific events within the gait cycle. For example, it allows comparison of the values of the lowest point achieved by the center of gravity in *Ateles* and *Lagothrix*, even though this point is achieved during midsupport in the former and at the time of touchdown of the tail in the latter. Comparison of the extreme values of the variables and of the actual range of body positions and intersegmental angles facilitates analysis of the relationship between skeletal design and positions of the body and limbs. Maximum and minimum values for each variable were collected along with other data on each step. From this database the average minimum and maximum values as well as means were calculated. These data were tested for correlations with speed using conservative nonparametric Spearman correlation methods. Data that strongly and significantly correlated with speed were compared using a standard ANCOVA with the variable of interest as the dependent y-variable and speed the independent (effectively held constant) x-variable. This resulted in the calculation of an adjusted mean and standard error in which the effect of speed was accounted for. In all other cases a standard ANOVA was used. Third, point-by-point comparisons of specific variables provided a general sense of overall change during a stride as well as data on variation in timing during the cycle. For example, the specific variables used to evaluate pendular movement were analyzed point-by-point by using ANCOVA or ANOVA as appropriate for the variable. Since the actual speed of brachiation in *Lagothrix* and *Ateles* did not differ significantly, the results of ANCOVA and ANOVA tests showed the same pattern of significant versus non-significant differences between the two species. In all comparisons significance was recorded at the level of $P < 0.05$.

RESULTS

Tail Use and Free Flight

Frame-by frame analysis reveals both similarities and differences in the bi-manual locomotion of *Lagothrix* and *Ateles* (Fig. 2A,B). In both species the prehensile tail plays an active role in suspensory locomotion. The relationship between hand and tail contacts during brachiation along a single support, however, differs significantly between the two species. In *Lagothrix*, a typical (95% of strides) brachiation sequence includes a tail grasp in association with every hand grasp, which results in a very uniform, but choppy, pattern of progression. In *Ateles*, on the other hand, the tail usually (72% of strides) grasps with every other hand hold, which results in a more flowing progression. G-test results showed that the use of the tail only with alternate hand holds in 72% of *Ateles*

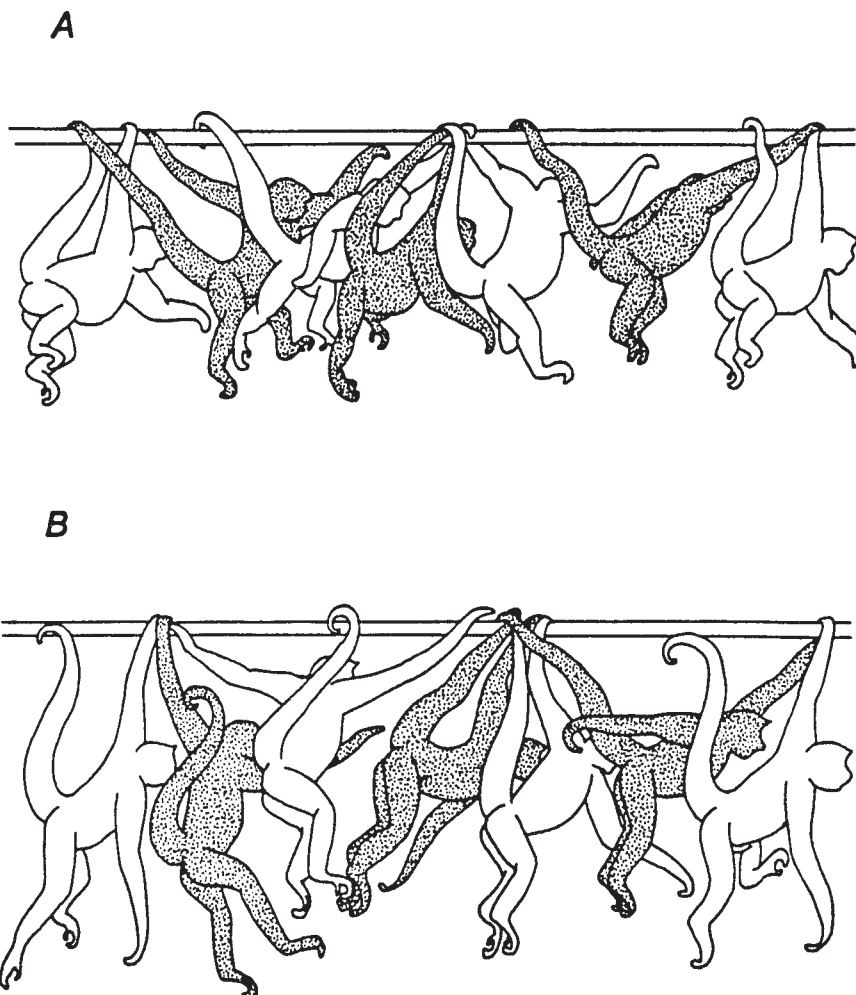


Fig. 2. Typical brachiation sequences showing one complete stride. **A:** *Lagothrix* (tail hold accompanies each hand hold). **B:** *Ateles* (tail hold accompanies alternate hand holds). Although the two sequences begin with opposite hand holds, the individual drawings in each show similar events in the gait cycle. Drawing 1 midsupport of a hand; drawings 2, 3 and 5, 6 liftoff of trailing hand, free-flight phase, and touchdown of leading hand; drawing 4 simultaneous support by hand and tail; drawing 6 touchdown of leading hand; and drawing 7 midsupport of a hand, similar to drawing 1. Note the differences in the angle of the body relative to tail use in the two species (drawn by Dionisios Youlatos from tracings of videorecordings).

vs. in 5% of *Lagothrix* strides was a highly significant difference between the species. The order of recorded events in each type of stride is shown below. TD indicates touchdown (grasping of the support), MS is midsupport (the most proximal joint of the extremity is positioned vertically below the grasping appendage), LO is liftoff (release of the support), L is left hand, R is right hand, and T is tail. A typical sequence using the tail with every hand hold is TD-L; TD-T; MS-L; MS-T; LO-L; LO-T; TD-R; TD-T; MS-R; MS-T; LO-R; LO-T; TD-L. A typical sequence using the tail with alternate hand holds is TD-L; TD-T; MS-L; MS-T; LO-L; LO-T; TD-R; MS-R; LO-R; TD-L. In both sequences, liftoff of the trailing hand (the hand positioned behind the body) precedes liftoff of the tail and liftoff of the tail

precedes touchdown of the leading hand (the hand reaching forward in advance of the body) (see Fig. 2A drawings 2, 3 and 5, 6, and Fig. 2B, drawings 5, 6). In steps without a simultaneous tail hold, liftoff of the trailing hand precedes touchdown of the leading hand (see Fig. 2B, drawing 3). Thus both types of brachiation sequences potentially have free-flight. This period of free-flight, however, is sometimes less than 1/30th of a sec.

Temporal Gait Variables

Table I presents gait variables related to temporal components of *Lagothrix* and *Ateles* brachiation. There is no significant difference in speed between the two species. When stride length and stride frequency are adjusted to take into account limb length (brachium plus antebrachium), adjusted stride length is still significantly greater in *Ateles* and adjusted stride frequency is still significantly greater in *Lagothrix*. Thus, observed differences in the brachiation of *Lagothrix* and *Ateles* are not the result only of differences in either speed or size.

Features of brachiation in which *Ateles* significantly exceeds *Lagothrix* are stride length (distance traveled each stride), stride duration (elapsed time during each stride), and both the support and swing (non-support) phase durations within a given stride. Features in which *Lagothrix* significantly exceeds *Ateles* are stride frequency per unit time and the proportion of each stride in which both hands, but not necessarily the tail, are simultaneously in swing phase (no-hand phase/stride duration). To obtain the same speed, *Ateles* uses longer, slower strides with greater periods of support by each hand than does *Lagothrix*. *Lagothrix*, on the other hand, uses shorter, more frequent strides with greater periods of neither hand, but not necessarily the tail, in contact with the support. *Ateles* brachiation is achieved by long, fluid strides with longer hand holds, while *Lagothrix* utilizes short, choppy strides with quick hand holds.

The brachiation of *Lagothrix* and *Ateles* have in common many characteristics related to speed and stride as evidenced in Table II. The direction of change in all variables with speed is the same in the two species. With increased speed, both species significantly increase the stride length and the proportion of each stride in which both hands, but not necessarily the tail, are simultaneously in

TABLE I. Temporal Gait Variables*

Variable	Lagothrix	Ateles	Significances
Speed (m/s)	1.43 (.24)	1.59 (.28)	ns
Stride length (m)	1.64 (.19)	2.44 (.4)	***
Adj. stride length (SL/forelimb)	.049 (.006)	.056 (.009)	***
Stride frequency (strides/second)	.865 (.1)	.67 (.1)	***
Stride duration (secs)	1.17 (.14)	1.52 (.22)	***
(support + swing + two no-hands)			
Adj. stride frequency (SF/forelimb)	.026 (.003)	.015 (.002)	***
Support phase duration (secs)	.44 (.08)	.64 (.12)	***
Duty factor (contact time/stride duration)	.37 (.04)	.41 (.02)	ns
Swing phase duration (secs)	.73 (.08)	.89 (.11)	***
Swing phase/stride duration	.62 (.04)	.58 (.02)	ns
No-hands phase duration (secs)	.17 (.08)	.14 (.03)	ns
No-hands phase/stride duration	.18 (.03)	.09 (.008)	***

*Mean and 1 standard deviation (in parenthesis).

*** $P < .05$.

TABLE II. Spearman Correlation Coefficients for Temporal Gait Variables with Speed

Variables	Lagothrix	Ateles
Stride length	.81***	.62***
Stride frequency	.53***	.58
Stride duration	-.45	-.57
Support phase duration	-.72***	-.47***
Duty factor (support phase/stride duration)	-.72***	-.37
Swing phase duration	-.34	-.51***
Swing phase/stride duration	.69***	.33
No-hands duration	.44	.39
No-hands phase/stride duration	.51***	.65***

*** $P < .05$.

swing phase (no-hands phase/stride duration). Actual stride duration does not decrease significantly with speed in either species but actual support phase duration does. Despite overall similarities in the effect of speed, the significance of some of the adjustments differ in the two species. For example, as speed increases, *Lagothrix* significantly increases its stride frequency as well as significantly decreases the proportion of a stride in which the hand is in contact with the support (Duty Factor) (Fig. 3) and conversely significantly increases the proportion of swing phase relative to stride duration. This shift in proportions as speed increases is the result of a significant decrease in support phase duration without significant change in swing phase duration. *Ateles*, on the other hand, with increased speed does not significantly alter the proportion of either the support (Duty Factor) or the swing phase relative to stride duration. Instead, with increased speed *Ateles* significantly reduces both support and swing phase dura-

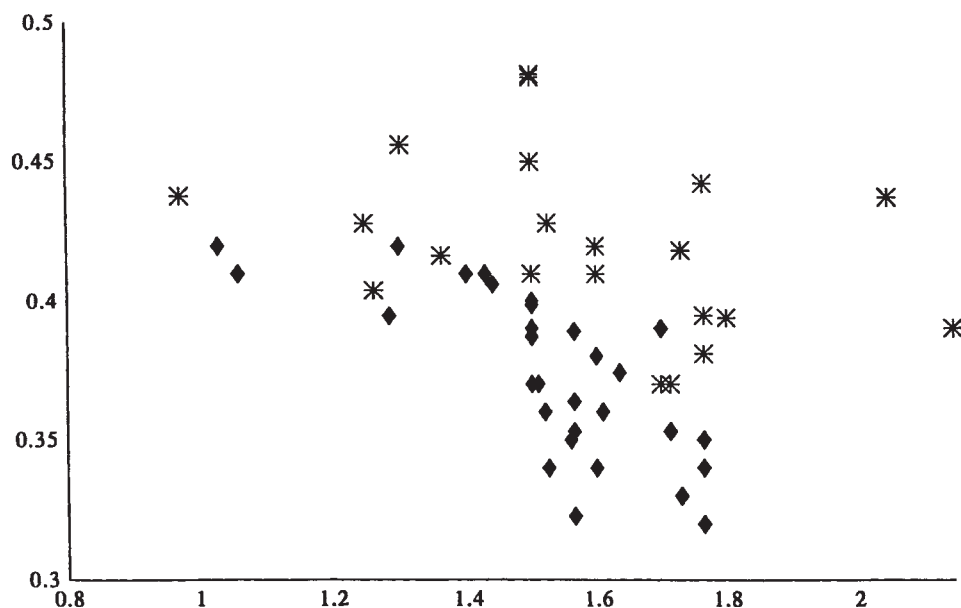


Fig. 3. Duty factor vs. speed. Duty factor is along the y-axis and speed (m/sec) the x-axis. *Lagothrix* is represented by black diamonds and *Ateles* by stars.

tion in the gait cycle and thus its Duty Factor and the swing phase to stride duration ratio are not significantly reduced (Table II, Fig. 3).

Both *Lagothrix* and *Ateles* are capable of consistently achieving brief periods of free-flight during bimanual locomotion. The no-hands phases in Tables I and II include both periods of tail only support and periods of free-flight. As seen in Figure 2 (see Fig. 2A, drawings 2, 3 and 5, 6, and Fig. 2B, drawings 3 and 5, 6), the presence and length of the period of free-flight is directly correlated with tail use. In steps with an accompanying tail hold the period of free-flight is very brief (usually one frame, 1/30th sec). In steps without an accompanying tail hold, the period of free-flight is longer (usually six frames, 1/5th sec). Thus both types of brachiation sequences potentially have free-flight but the duration of this period varies greatly depending on tail use, i.e., the presence or absence of an accompanying tail hold. No-hands duration does not differ significantly in either species with increased speed but, in both, the no-hands phase duration relative to stride duration is significantly increased with increased speed. Although neither species achieves the extreme pendulum effect and long period of free-flight of a gibbon in fast ricochet brachiation [Jungers & Stern, 1980, 1984; personal observation), both *Lagothrix* and *Ateles* consistently demonstrate effective brachiation and pendular motion in captivity.

Body Orientation and Tail Use Patterns

Just as tail use and overall characteristics of brachiation differ between the two species so too does body orientation and the use of the forelimbs. Maximum and minimum values during the support phase of brachiation are presented in Table III for those variables that affect the pendulum length of the body during brachiation. Pendulum length itself is presented as a percentage of body plus

TABLE III. Minimum and Maximum Values Compared by Genus and Tail Use Pattern*

Variable	Lagothrix (L)	Ateles not using tail (NT)	Ateles using tail (T)	Significant comparisons ($P < .05$)
Min. support shoulder	185.48 (4.7)	187.3 (11.4)	234.9 (19.4)	T:L, T:NT
Max. support shoulder	285.4 (8.25)	290.6 (14.8)	282.6 (12)	None
Min. support elbow	150.5 (6.7)	146.6 (14)	156.2 (9.3)	None
Max. support elbow	179.9 (4.2)	179.3 (3.3)	164.9 (4.2)	T:L, T:NT
Min. body angle	35.7 (6.4)	26.8 (4)	15.8 (7.6)	All
Max. body angle	65.6 (4.6)	71.8 (9)	51.67 (4.4)	T:L, T:NT
Range of body motion (max. - min. body angle)	29.9 (5.6)	45.02 (11.3)	35.87 (10.2)	L:NT
Min. tail-body angle	64.9 (9)	37.98 (12)	55.97 (5.4)	L:NT T:NT
Max. tail-body angle	108.8 (11)	96 (12.5)	99.2 (8.6)	L:NT
Min. proximal-distal tail angle	123.9 (5.8)	117.16 (8.6)	143.49 (6)	L:T, T:NT
Max. proximal-distal tail angle	166.3 (6.2)	159.2 (12)	169.8 (8.1)	None
Min. pendulum length (% body + forelimb)	.56 (.04)	.572 (.065)	.636 (.05)	T:L, T:NT
Max. pendulum length (% body + forelimb)	.87 (.064)	.922 (.08)	.83 (.069)	T:L, T:NT

*Mean and 1 standard deviation (in parenthesis).

forelimb length to minimize the effect of species size differences. All sequences were adjusted for speed to eliminate this variable from the analysis. Since *Lagothrix* uses a new tail hold with every hand hold, its gait is very symmetrical and only one value is presented for each variable. *Ateles*, on the other hand, usually uses a tail hold with only alternate hand holds and thus its gait is asymmetrical. Data for *Ateles* steps with and without a simultaneous tail hold are presented separately to indicate variables which differ markedly in these two types of support phases.

Total range of body motion (maximum minus minimum body angle) and maximum pendulum length (as a percentage of body length plus forelimb length) appear to be influenced more by tail use than by species. At no time during a stride does the minimum body angle of *Lagothrix* achieve the degree of horizontality (smaller body angle) demonstrated in *Ateles* regardless of tail use. Not only is *Lagothrix* significantly less horizontal than *Ateles* but also within *Ateles* there is a significant difference between steps with and steps without a simultaneous tail hold (see Fig. 2). Since the minimum angle at the support shoulder occurs either at the time of touchdown or midsupport of the hand, these differences in the orientation of the body axis are reflected in the minimum angle of the support shoulder. The body of *Ateles* in steps with an accompanying tail hold is more horizontal at the time of touchdown and thus the minimum angle of the support shoulder is greater in these steps than in either *Lagothrix* or *Ateles* steps without an accompanying tail hold. It is notable that for many of the variables associated with body positioning (e.g., minimum support shoulder, maximum support elbow, and maximum body angle), *Lagothrix*, which uses a new tail hold with every hand hold, more closely resembles *Ateles* in steps without a simultaneous tail hold rather than *Ateles* in steps with a simultaneous tail hold.

The minimum angle between the base of the tail and the body axis (tail-body angle) is significantly smaller in those steps where a tail hold does not accompany the hand hold. In these steps the tail more closely parallels the body axis as the tail reaches in advance of the fixed hand to secure a grip further forward along the line of motion. The event in the gait cycle where maximum or minimum values occur may vary from step to step as well as with use of the tail and/or species.

Pendulum Length and Body Angle in Support Phase

Data on pendulum length as a percentage of body length plus forelimb length and body angle at important events in support phase of the gait cycle are presented in Table IV. The events noted are: touchdown of a hand, touchdown of the tail, midsupport of a hand, midsupport of the tail, and liftoff of a hand. These results are presented by species and, in the case of *Ateles*, by tail use and the significance of differences between events is noted. The results on pendulum length are also plotted in Figure 4. *Ateles* steps that are not accompanied by a tail hold (not using tail) show the greatest change in pendulum length during a step and also achieve a greater pendulum length. Pendulum length in both *Ateles* with an accompanying tail hold (using tail) and *Lagothrix* are almost identical both at touchdown and liftoff. Maximum pendulum length in *Lagothrix* is usually at touchdown of the tail while maximum pendulum length in *Ateles* in steps accompanied by a tail hold is usually later in the support phase, at midsupport of the tail. The minimum and maximum numbers seen in Table III may differ from the numbers in Table IV since minimum/maximum values do not always occur at the same point in every gait cycle and they may, or may not, coincide with a major

TABLE IV. Pendulum Length and Body Angle Compared by Point in Support Phase*

Pendulum length (% forelimb + body)	Touchdown (TD)	TD-Tail	Midsupport (MS)	MS-Tail	Liftoff (LO)	Significant ($P < .05$) comparisons
Ateles not using tail	.57 (.07)	—	.89 (.08)	—	.71 (.07)	MS:LO, MS:TD, LO:TD
Ateles using tail	.63 (.04)	.68 (.07)	.77 (.05)	.85 (.07)	.70 (.08)	MST:LO, MST:TDT, MST:TD, MS:TD
Lagothrix	.62 (.07)	.81 (.10)	.80 (.08)	.76 (.03)	.70 (.04)	MST:TD, LO:TDT, LO:MS, LO:TD, TD:TDT, TD:MS

Body angle	Touchdown (TD)	TD-Tail	Midsupport (MS)	MS-Tail	Liftoff (LO)	Significant comparisons
Ateles not using tail	31 (8)	—	46 (6)	—	72 (8)	TD:MS, TD:LO, MS:LO
Ateles using tail	34 (6)	19 (11)	25 (9)	45 (3)	51 (5)	LO:TDT, MS:LO, MST:MS, MST:TDT
Lagothrix	45 (8)	50 (6)	48 (11)	45 (7)	59 (8)	LO:MS, LO:MST, LO:TD

*Mean and 1 standard deviation (in parenthesis).

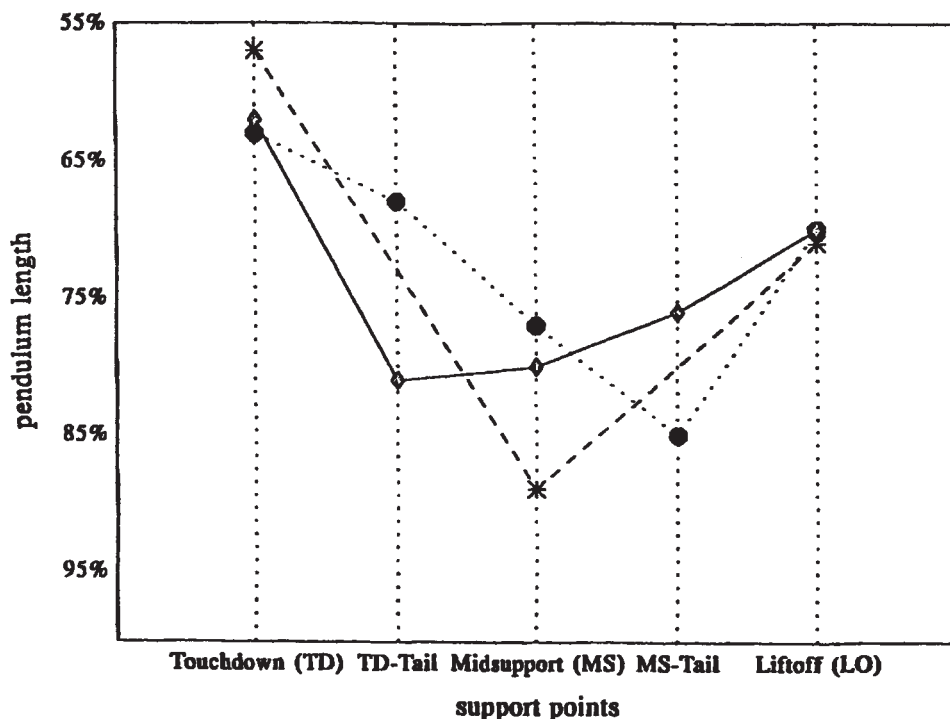


Fig. 4. Pendulum length as a percentage of forelimb plus body length during critical events in the support phase of a single step. Pendulum length is along the y-axis; events during support phase along the x-axis; symbols indicate means. *Lagothrix* (gray diamond) strides are symmetrical, a tail hold accompanies every hand hold, and all steps are similar; *Ateles* strides are asymmetrical and steps in which a hand hold is accompanied by a tail hold (black circle) differ from steps in which the hand hold is not accompanied by a tail hold (star). Compare this to Figure 2A,B, and to Table IV.

event, e.g., touchdown, liftoff, and midsupport. Tail use significantly affects the length of the pendulum in *Ateles* resulting in marked differences in pendular motion between steps with simultaneous tail holds and steps without simultaneous tail holds.

Differences in body angle during various events in the gait cycle appear to be in part determined by tail use and in part by species (Table IV; Fig. 5). At touchdown of any of the three appendages (either hand or the tail), the body of *Lagothrix* is significantly more vertical than that of *Ateles* regardless of tail use. At midsupport of the hand, the body angle of *Ateles* during a step cycle with a simultaneous tail hold (using tail) is significantly more horizontal than that of *Lagothrix* or of *Ateles* without a simultaneous tail hold (not using tail). At liftoff of the hand, the body of *Ateles* without a simultaneous tail hold is significantly more vertical than *Ateles* with a simultaneous tail hold. At this point in the gait cycle the body angle of *Lagothrix* lies between these two values for *Ateles* but it is more similar to *Ateles* with a simultaneous tail hold. These differences in body angles at liftoff reflect the effect of a grasping tail on body angle.

In all strides elbow flexion occurred between midsupport and liftoff during the support phase but the amount of elbow flexion was statistically significant only in *Lagothrix*. Elbow flexion prior to liftoff of the trailing hand not only raises the body in preparation for touchdown of the leading hand but also has the po-

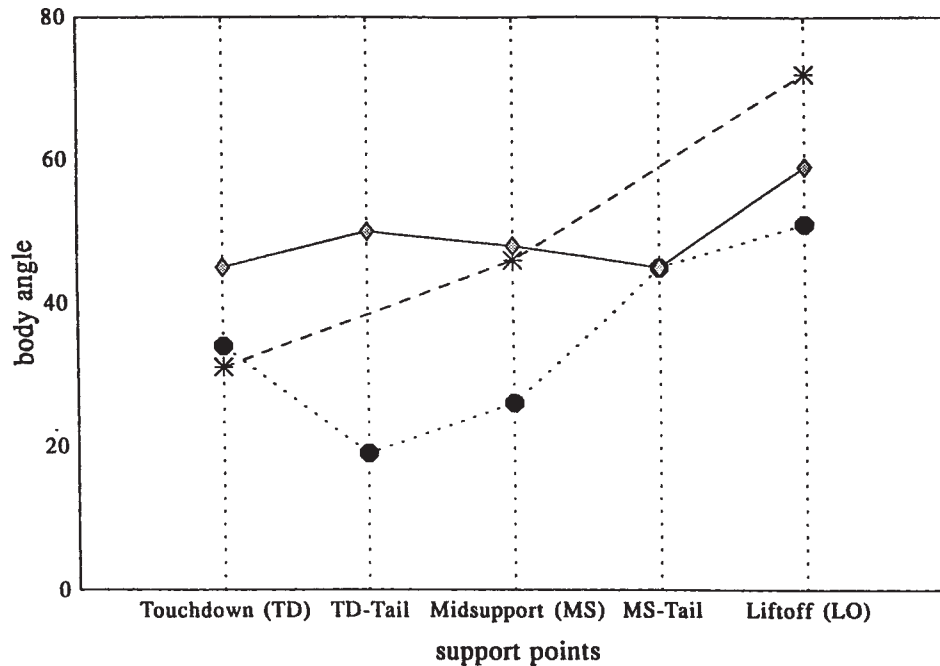


Fig. 5. Body angle (in degrees) during critical events in the support phase of a single step. Body angle below the brachiation pole is along the y-axis; events during support phase along the x-axis; symbols indicate means. 0° represents horizontal body orientation; 90° represents vertical body orientation. *Lagothrix* (gray diamond) strides are symmetrical, a tail hold accompanies every hand hold, and all steps are similar; *Ateles* strides are asymmetrical and steps in which a hand hold is accompanied by a tail hold (black circle) differ from steps in which the hand hold is not accompanied by a tail hold (star). Compare this to Figure 2A,B, and to Table IV.

tential of contributing to the momentum of the cycle. The angles of flexion of the hip and knee remain relatively constant throughout the gait cycle and thus do not appear to contribute to any pumping activity. The use of the lower limb does not differ significantly either with species or tail use.

The angle at the base of the tail (tail-body angle) at both touchdown and liftoff is significantly smaller in *Ateles* steps without a simultaneous tail hold than in either *Ateles* steps with a simultaneous tail hold or *Lagothrix*. At midsupport, the value of the angle of the base of the tail for *Lagothrix* is between the values seen in *Ateles* with or without a simultaneous tail hold. The significant difference, however, is between steps with or without a simultaneous tail hold, not between species (see Table III). Species differences in the angle of the base of the tail become evident when the tail itself touches down or is in midsupport. During these events the angle at the base of the tail is significantly less in *Ateles* than in *Lagothrix*. In general, the angle of the midsection of the tail (proximal-distal tail angle) is similar in steps with simultaneous tail holds regardless of species and is significantly different in *Ateles* steps without a simultaneous tail hold. The only exception to this is in midsupport where the rest of the tail is significantly more flexed in *Ateles* during steps with a simultaneous tail hold than in either *Ateles* without a simultaneous tail hold or *Lagothrix*. At this point in the gait cycle *Ateles* body is also more horizontal (smaller body angle) in steps with a simultaneous tail hold. Thus the tail appears to be raising the body thereby contributing to its pendular momentum.

DISCUSSION

Although *Ateles* has long been recognized as an efficient brachiator in captivity, this study has found that its closest relative, *Lagothrix*, has similar capabilities. Despite overall similarities in the brachiation of these two prehensile tailed atelines, many aspects of their actual performance differ significantly. In addition to differences that can be attributed to species, results also show significant variation between steps in which the hand hold is accompanied by a simultaneous tail hold and those in which it is not. Some variables, such as minimum body angle, were found to vary significantly both by species and by tail use.

The observed pattern for captive brachiation in *Ateles* (see Fig. 2B) is similar to that depicted in Jungers and Stern [1981] and Jenkins et al. [1978] with the exception of the greater distance between the tail hold and hand hold in the latter. The latter study also noted that *Ateles* used alternate tail holds only at slower speeds (3–4 km/hr) and demonstrated no clear preference as to which hand (right or left) moved in synchrony with the tail. Speeds in the current study are similar to those of Jenkins et al. [1978] but *Ateles* brachiation is consistently (72% of strides) characterized by use of a tail hold with alternate hand holds. No obvious preference is shown as to which hand is synchronized with the tail. *Lagothrix* (see Fig. 2A), on the other hand, almost without exception (95% of strides), uses a new tail hold with every hand hold. Thus, the overall rhythm of brachiation differs greatly between the two species. As noted in Table I, speed did not vary significantly between the species and thus was not a source of the observed differences. Adjustment of stride length and frequency to take into account different limb lengths did not affect significance and thus size differences do not explain observed species differences in brachiation.

In the current study, both *Lagothrix* and *Ateles* consistently demonstrated an aerial or free-flight phase [called glide period by Carpenter, 1976] in which none of the appendages were grasping the support. Since the tail consistently releases the support after the trailing hand, the free-flight phase was longest when the trailing hand was not accompanied by a tail hold. The time of this aerial phase, however, was shorter than that seen in ricochet brachiation in *Hylobates* [Jungers & Stern, 1980, 1984; personal observation]. Although both ateline species may lack the "simple consistent two-phase rhythm" [Preuschoft & Demes, 1984, p 99] of *Hylobates*, both are capable of sustaining clearly established rhythms of motion that incorporate coordinated movements of the tail and forelimbs into either a one tail hold per step or a one tail hold per stride pattern of brachiation.

With increasing speed, *Lagothrix* significantly alters the proportion of support and swing phases in a stride by significantly decreasing the duration of support while preserving swing phase duration. The gaits of quadrupedal primates and other mammals show a similar pattern, i.e., significant reduction in the support phase with little reduction in the swing phase as speed increases [Hildebrand, 1967; Prost, 1965; Vilensky, 1983; Vilensky & Gehlsen, 1984]. The pattern seen in *Ateles*, however, differs from this in that the duration of both phases of the gait cycle are significantly reduced as speed increases. The more symmetrical reduction in the two phases does not result in significant changes in the proportion of one to the other in the gait cycle. This pattern of no significant reduction in duty factor (support time as a proportion of stride time) with increased speed has previously been reported for human runners who increase their contact time by flexing their hips and knees and thus do not significantly decrease the proportion of support phase

[McMahon et al., 1987]. The combination of non-significant reduction in duty factor with the longer support duration in *Ateles* brachiation suggests a relationship between pendular body motion and contact. A long pendulum which swings through a larger angular excursion will have a longer contact time [Blickhan, 1989]. This longer contact allows a longer period for the application of force to the substrate and results in lower peak vertical force on the substrate. This may help relieve stress on the forelimb and reduce oscillations of the substrate. Such a pattern has been demonstrated for primate quadrupeds [Schmitt, 1995]. Further investigation will demonstrate whether this pattern holds for arm-swinging primates as well.

The significant differences between *Lagothrix* and *Ateles* found in this study in the uprightness and angular movement of the body axis during brachiation may contribute to understanding differences in the recruitment of shoulder musculature as reported by Stern et al. [1980]. Differences in body position are not only significant between species but also between steps in *Ateles*, which are, or are not, accompanied by a simultaneous tail hold. Since the liftoff of the hand precedes liftoff of the tail, the tail has considerable influence over body orientation and appears capable of retarding and lifting the body, a phenomenon also noted by Jenkins and colleagues [1978]. As shown in Figure 2 and Tables III and IV, significant differences in the orientation of the body, particularly at touchdown of the leading hand, can be directly correlated with differences in use of the shoulder. Furthermore, the range of motion in the shoulder of *Lagothrix*, which uses a tail hold with every hand hold, is more similar to *Ateles* in steps without an accompanying tail hold than to *Ateles* steps with one. Thus, the influence of the tail in New World monkey brachiation appears to be far more complex than implied by Stern and colleagues [Stern et al., 1980; Jungers & Stern, 1981] who referred to the use of the tail during brachiation as a “fail-safe mechanism” to be used as a safety rope if the grasping hand failed to reach the next support. The frequent use by *Ateles* of tail grasps with only alternate hand holds as well as the markedly different effects of tail use in *Ateles* and *Lagothrix* demonstrate that the prehensile tail in these species is an active component of brachiation, not just a safety mechanism.

A recent study of the musculature of both prehensile and nonprehensile tails in New World monkeys [Lemelin, 1995] demonstrates that the two types of tails differ morphologically. Furthermore, it found that within the prehensile tailed group, the musculature of *Ateles* differed from that of *Lagothrix*. On the basis of soft tissue morphology, Lemelin predicted that *Ateles* has the ability to “hyperextend” the tail. Osteological observations during the current study suggest that this capability in *Ateles* results from two features. The sacral articular surface for the sacrocaudal joint faces distodorsally rather than distally, producing a partial extension set to the base of the tail. Also, there are a greater number of relatively shorter caudal vertebrae that fully articulate with each other than in *Lagothrix*. During brachiation this “hyperextension” is evidenced by the low minimum tail-body angle observed during *Ateles* steps without an accompanying tail hold (Fig. 2B, drawings 2, 3; Table III). Thus, it may be possible to correlate muscular [Lemelin, 1995] and osseous differences in these two prehensile tailed species with observed differences in tail use during brachiation.

The increase in elbow flexion between midsupport and liftoff of the hand (5–20° in any given step were observed in this study) “puts energy into the ‘pendulum’ to make up for that lost to friction and air resistance” [Fleagle, 1977, as quoted by Larson & Stern, 1986]. Elbow flexion in the latter half of the support

phase also raises the center of gravity resulting in greater gravitational acceleration in the following gait cycle [Stern et al., 1980; Jungers & Stern, 1984]. In this study, the increase in elbow flexion between midsupport and liftoff is significant in *Lagothrix*. In *Ateles*, although elbow flexion occurs both in steps with, and without, a simultaneous tail hold, the degree of flexion was not found to be significant in this study. A partial explanation for the lack of need for significant elbow flexion in *Ateles* may be that animals with long limbs do not need to flex as much as those with short limbs in order to achieve the same lift in height [Preuschoft & Demes, 1984].

A potential source of additional energy for the pendular system may possibly be associated with changing body orientation. Tables III and IV demonstrate considerable change in body orientation during ateline brachiation. In the second half of support phase the body orientation becomes more vertical. Between liftoff of the trailing hand and touchdown of the leading hand, i.e., during the phase when there is no hand in contact with the support, the orientation of the body undergoes considerable change (see Fig. 2A, drawings 2, 3 and 5, 6; 2B, drawings 3, 4 and 5, 6; as well as Fig. 5). At the time of touchdown the body is more horizontal than at the time of the liftoff which immediately preceded it. This "falling forward" of the body during the no-hands phase may be capable of adding energy to the system, particularly in steps that lack a simultaneous tail hold and thus have a longer period of free-flight. This source of potential energy has not been previously described in brachiation and requires further analysis of its potential. At the same time that the body is "falling forward," the swing arm is also moving rapidly downward away from the previous hand hold and it too may be supplying momentum. Kinematic analysis of hindlimb movements during brachiation of *Ateles* [see also Jenkins et al., 1978] and *Lagothrix* does not indicate that either species utilizes the marked "pumping" activity described in siamangs [Fleagle, 1974] and thus the hindlimbs are probably not a potential source of energy in ateline brachiation.

During brachiation, the orientation of the body (body angle) differs significantly between *Lagothrix* and *Ateles* as well as between *Ateles* with, or without, a simultaneous tail hold (Table III). A comparison of drawings of brachiation sequences of *Lagothrix* and *Ateles* (Fig. 2A,B) with similar drawings of *Hylobates* [Fig. 5, Larson, 1988] illustrates that the body orientation of the latter is more vertical throughout the brachiation sequence. Thus, differences in pendular activity in brachiation between atelines and hylobatids appear to be not only the difference between a double and a single pendulum but also the difference between a nonlinear and a nearly linear pendulum. The ability of *Ateles* to frequently maintain overhead hand holds with the body in a horizontal or near-horizontal position is made possible by features of its shoulder region that are not found in *Lagothrix*. These include a "hominoid-like" scapula and proximal humerus in which the spine and glenoid of the scapula are directed relatively cranially (affecting the orientation of the scapulothoracic and scapulohumeral joints, and the line of action of the scapulohumeral musculature) and a relatively globular humeral head that exhibits a relatively high degree of torsion (affecting the amount of movement at the scapulohumeral joint, and the angular positioning of the forelimb with respect to the trunk).

This analysis of pendular motion during brachiation of *Lagothrix* and *Ateles* demonstrates that in captivity both species readily perform proficient brachiation with very brief periods of free-flight. Whether or not these morphologically and behaviorally feasible locomotor patterns are used consistently in their natural habitat is the topic of another paper [see Cant et al., 1996].

CONCLUSIONS

1. In captivity, both *Lagothrix* and *Ateles* demonstrate effective brachiation with brief periods of free-flight and pendular motion.
2. Brachiation in *Lagothrix* and *Ateles* differ significantly in the use of the prehensile tail, stride length, stride frequency, and length of hand holds.
3. The body of *Lagothrix* is significantly more vertical during brachiation than that of *Ateles*. The angle of the body in *Ateles* differs significantly with tail use.
4. During brachiation overall pendulum length in *Lagothrix* is shorter than in *Ateles*. Pendulum length in *Ateles* differs significantly with tail use.
5. The role of the prehensile tail in atelines is much more complex than previously thought and its use strongly influences the kinematics of brachiation.
6. *Lagothrix* brachiation is less hylobatid-like than that of *Ateles*. This parallels morphological findings that similarities between hylobatids and *Lagothrix* are fewer and less pronounced than those of *Ateles*.

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