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Lateral bending of the lumbar spine during quadrupedalism in strepsirhines

Much research has been devoted to spinal kinematics of non-mammalian vertebrates, while comparatively little is known about the locomotor role of spinal movements in mammals, especially primates. This study, conducted at the Duke University Primate Center, examines the function of lateral spinal bending during quadrupedal walking among a diverse sample of strepsirhines. The taxa studied include *Loris tardigradus* (1), *Nycticebus coucang* (1), *N. pygmaeus* (1), *Cheirogaleus medius* (2), *Varecia variegata* (2), *Eulemur fulvus* (2), and a total sample size of 261 strides. Lateral bending varies among the taxa with respect to both magnitude and effects of velocity, and does not appear to be correlated with body size. In addition, the timing of lateral bending during a stride appears to differ from that reported for other (nonmammalian) tetrapods. On average, maximum lateral flexion occurs just after ipsilateral foot touchdown, which may be functionally associated with touchdown of the contralateral forelimb during diagonal sequence gait. For some of the taxa, lateral flexion coincides more closely with foot touchdown as velocity increases, suggesting a functional role in increasing hindlimb stride length. Both of these timing patterns contrast with those reported for lizards. Finally, although lorids as a group have been described as having a "sinuous" gait, this study shows more pronounced lateral flexion in *Nycticebus* than in *Loris*.

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Introduction

In recent years, much research has been devoted to the kinematic and kinetic aspects of locomotion as a means to understand the function and evolution of musculoskeletal features in primates. For the most part, this type of research has focused on limb function (e.g., Joffroy *et al.*, 1990; Meldrum, 1991; Tuttle *et al.*, 1992; Demes *et al.*, 1994, 1995; Schmitt & Larson, 1995; Schmidt & Fischer, 2000), while much less is known about the functional role of spinal movements in primate locomotion (but see Hurov, 1987; Demes *et al.*, 1990; Vilensky *et al.*, 1994; Preuschoft *et al.*, 1995; Schmidt & Fischer, 2000). In fact, most detailed, quantitative investigations of spinal kinematics have focused on nonmammalian

vertebrates (e.g., Roos, 1964; Urban, 1965; Daan & Belterman, 1968; Sukhanov, 1974; Edwards, 1985; Webb & Blake, 1985; Sigvardt, 1989; Carrier, 1990; Ritter, 1992, 1995, 1996; Frolich & Biewener, 1992; Ashley-Ross, 1994a,b; Long *et al.*, 1994; Jayne & Lauder, 1995a,b, 1996; Gillis, 1997, 1998; Reilly & Delancey, 1997a,b; O'Reilly *et al.*, 1997, 2000), while fewer comparative data are available for mammals (but see Hildebrand, 1959; Goslow *et al.*, 1973; Jenkins, 1974; Carlson *et al.*, 1979; English, 1980; Halpert *et al.*, 1987; Alexander, 1988; Pridmore, 1992; Fischer, 1994; Schilling & Fischer, 1999; and primate references above). This is surprising, considering the fact that one of the key innovations in the evolution of mammalian locomotion was the shift to an

emphasis on sagittal, rather than lateral, movements of the spine (Hildebrand, 1974).

For many mammals, sagittal bending of the spine increases stride length, particularly when asymmetrical gaits such as galloping are used at faster speeds (Hildebrand, 1959, 1974; Howell, 1965; Goslow *et al.*, 1973; English, 1980). This adaptation is quite distinct from that of most other terrestrial tetrapods, which exhibit lateral bending during locomotion (Sukanov, 1974; Carrier, 1990; Frolich & Biewener, 1992; Ritter, 1992, 1995; Ashley-Ross, 1994*a,b*). This basic contrast is well known, but studies on mammals also have revealed variation in spinal flexibility across species, gaits and speeds (e.g., Hildebrand, 1959; Goslow *et al.*, 1973; Carlson *et al.*, 1979; English, 1980). In fact, Pridmore's (1992) study of an opossum (*Monodelphis domestica*) demonstrated that lateral bending of the trunk continues to be an important component of mammalian locomotion, particularly at slower walking speeds (see also Carlson *et al.*, 1979). Clearly, more research is needed to explore the functional role of the mammalian spine during locomotion. This is especially true for primates, for which we know much about vertebral morphology (Mivart, 1865; Schultz, 1961; Erikson, 1963; Ankel, 1967, 1972; Benton, 1967, 1974; Rose, 1975; Ward *et al.*, 1993; Shapiro, 1993*a,b*, 1995; Sanders & Bodenbender, 1994; Johnson & Shapiro, 1998; Sanders, 1998), and little about actual movements of the spine during locomotion.

The purpose of this study was to investigate the role of lateral bending of the spine during quadrupedalism in a broad sample of strepsirhines. Although strepsirhines exhibit significant differences in vertebral morphology in accordance with their positional behavior (Mivart 1865; Straus & Wislocki, 1932; Schultz, 1961; Ankel, 1967, 1972; Cartmill & Milton, 1977; Gebo, 1989; Ravololonarivo, 1990; Kumakura &

Inokuchi, 1992; Shapiro, 1993*a*, 1995; Shapiro *et al.*, 1994; Majoral *et al.*, 1997; Simons, 1998; Simons & Shapiro, 1998), the relationship between vertebral morphological variation and spinal kinematics has not been tested empirically. For example, Ankel (1967) noted that the relatively horizontal orientation of the lumbar zygapophyses in lorids¹ suggests that these primates emphasize lateral, rather than sagittal movements of the spine during quadrupedal walking (see also Curtis, 1995). Indeed, lorid back movements have been described as "sinuous" or "serpentine" (Hill, 1953; Walker, 1969, 1974). Demes *et al.*'s (1990) quantitative analysis of lorid walking gaits also suggested that lorids use lateral flexion of the spine to increase stride length, but spinal movements were not measured directly. The contribution of lateral spine flexion to performance variables of other strepsirhines is unknown.

The goal of this quantitative kinematic analysis was to investigate the functional contribution of lateral spinal flexion to quadrupedal locomotion and to address three questions:

- (1) What are the effects of body size and velocity on the magnitude and timing of lateral spinal flexion in strepsirhines?
- (2) Are lorids unique compared to other strepsirhines? Specifically, do lorids utilize more pronounced lateral spinal flexion during quadrupedalism than do other strepsirhines?
- (3) How do strepsirhines compare to other vertebrates?

Materials and methods

Sample

Kinematic data were collected at the Duke University Primate Center. The sample

¹Taxonomy used here follows Yoder (1997).

Table 1 Sample

Species	Primary locomotor behavior	Body size (g)	Angle of lateral flexion at touchdown <i>N</i> (no. of strides)	Overall range of flexion <i>N</i> (no. of strides)	Bending-footfall delay <i>N</i> (no. of strides)
<i>Cheirogaleus medius</i> 1	Arboreal	240	53	72	72
<i>Cheirogaleus medius</i> 2	quadrupedalism	190	28	28	28
<i>Cheirogaleus medius</i> pooled	and leaping	Mean: 215	Total: 81	Total: 100	Total: 100
<i>Eulemur fulvus</i> 1	Arboreal	2320	24	24	24
<i>Eulemur fulvus</i> 2	quadrupedalism	2640	33	35	35
<i>Eulemur fulvus</i> pooled	and leaping	Mean: 2480	Total: 57	Total: 59	Total: 59
<i>Varecia variegata</i> 1	Arboreal	3130	37	37	37
<i>Varecia variegata</i> 2	quadrupedalism	3730	24	24	24
<i>Varecia variegata</i> pooled	and leaping	Mean: 3430	Total: 61	Total: 61	Total: 61
<i>Nycticebus pygmaeus</i>	Slow	470	18	18	18
<i>Nycticebus coucang</i>	quadrupedal	880	11	11	—
<i>Loris tardigradus</i>	climbing	189	12	12	—

Note: Sample sizes are based on strides, but during one complete stride there are two foot touchdowns on the same side. Due to variation between the two values for flexion at each touchdown of a stride, the two values were averaged for a single stride. In addition, three values were averaged for samples of two consecutive strides. This procedure avoids redundancy of data points because two consecutive strides share a touchdown. Thus, in some cases, sample sizes are smaller for angle at touchdown than for the other measurements (especially for *Cheirogaleus* 1).

included lemurids (*Eulemur fulvus* and *Varecia variegata*; two individuals of each), cheirogaleids (*Cheirogaleus medius*, two individuals), and lorids (*Loris tardigradus* and *Nycticebus coucang*; one individual of each). The taxa were chosen to represent a range of body sizes as well as locomotor preferences (Table 1). *Loris* and *Nycticebus* differ dramatically in positional behaviour from the other taxa. *Cheirogaleus*, *Eulemur* and *Varecia* predominantly utilize a combination of quadrupedalism and leaping for progression (Walker, 1974, 1979; Gebo, 1987; Pereira *et al.*, 1988; Oxnard *et al.*, 1990; Dagosto, 1994, 1995). The lorids do not leap; their locomotor repertoire consists of oblique, vertical and horizontal quadrupedal climbing, bridging, suspension, and cantilevering (Walker, 1969, 1974, 1979; Charles-Dominique, 1977; Dykyj, 1980; Glassman & Wells, 1984; Gebo, 1987; Oxnard *et al.*, 1990). Their quadrupedalism has been described as a steady “crawl”

(Jouffroy, 1989). For the purposes of this study, then, *Cheirogaleus*, *Eulemur* and *Varecia* are considered to be more similar to each other in positional behavior than any one of them is to the lorids (especially with regard to quadrupedalism). As indicated in Table 1, there is notable body size variation within each of these two main groups, which facilitates testing the effects of body size on spinal kinematics.

Experimental set-up

Small markers (5–10 mm, depending on the size of the subject) were placed at three locations along the lumbosacral region of the shaved back of each subject (Figure 1). Marker 1 was placed over the last thoracic vertebra, marker 2 over the last lumbar vertebra, and marker 3 over the last sacral vertebra. The last thoracic vertebra was located by palpating for the attachment of the last rib, the last lumbar vertebra was located by means of counting spinous

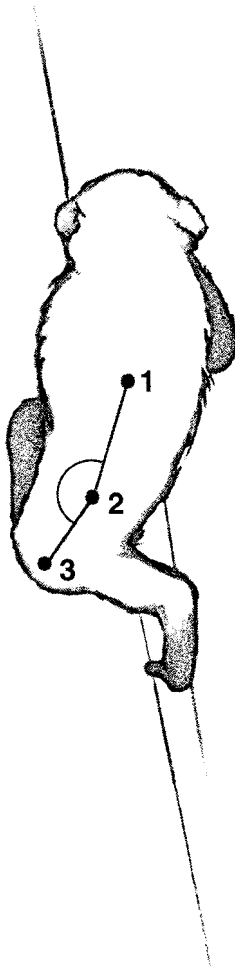


Figure 1. Location of markers and measurement of the angle of lateral flexion (*Nycticebus pygmaeus*). Marker 1=last thoracic vertebra, marker 2=last lumbar vertebra, marker 3=end of sacrum.

processes and/or palpating for a reduction in length of the spinous process at the first sacral vertebra, and (for taxa with a tail), the last sacral vertebra was palpated at its junction with the base of the tail. The distance between markers 1 and 2 spans the lumbar region, and the distance between markers 2 and 3 spans the sacrum. These marker locations exhibit minimal skin movement (Goslow *et al.*, 1973) and are therefore reliable areas for kinematic study (Schamhardt

et al., 1993). Due to loose skin in the cervical and upper thoracic regions (most likely for accommodating scapular movements), markers cannot be placed reliably above the last thoracic level, so these regions were not included in this study.

Each subject was videotaped with a Hi-8 camcorder (Canon L2) in overhead view moving across a horizontal wooden pole of 3 cm (*Loris*, *Nycticebus*, *Cheirogaleus*) or a plastic (PVC) pole of 5 cm (*Eulemur*, *Varecia*) diameter. Each pole was marked with lines 5 cm apart for scaling purposes. The recording frequency was 30 frames/second which is considered to be sufficient for animals moving in the speed range of our subjects (e.g., Demes *et al.*, 1990; Hamrick, 1996). A mirror was placed at an angle below the pole so that the hands and feet could be viewed at the same time as the spine. The view reflected in the mirror was used to identify step events (such as touchdown, toeff, etc.), but was not used for spinal measurements. Each subject was encouraged to move freely and at a variety of velocities. Only symmetrical gaits are included in this study. These include both walks and runs, in which hindlimb support phase is 50–90% or 20–50% of the stride duration, respectively (Hildebrand, 1967). The number of strides sampled for each individual is listed in Table 1, and the ranges of velocities sampled are listed in Table 2.

Measurements

Markers were digitized frame-by-frame using Motion Plus (Savvy Knowledge Systems Inc.) software designed specifically for motion analysis. Velocity was calculated as the displacement of Marker 1 in the direction of movement with respect to time, and is reported in cm/sec. Lateral flexion of the lumbar region (i.e., at the lumbosacral joint) was quantified by measuring the angle formed in a horizontal plane by the three markers, with the vertex at marker 2 (Figure 1). Lateral flexion *within* the

Table 2 Velocity ranges sampled (cm/s)

Species	Minimum velocity	Maximum velocity	Velocity range (maximum–minimum)
<i>Cheirogaleus medius</i> 1	29	168	139
<i>Cheirogaleus medius</i> 2	15	70	55
<i>Eulemur fulvus</i> 1	55	144	89
<i>Eulemur fulvus</i> 2	40	117	77
<i>Varecia variegata</i> 1	29	151	122
<i>Varecia variegata</i> 2	66	209	143
<i>Nycticebus pygmaeus</i>	10	98	88
<i>Nycticebus coucang</i>	40	109	69
<i>Loris tardigradus</i>	19	62	43

lumbar region was not measured due to the difficulty of accurately digitizing markers so close together, particularly in the smaller taxa. The angles were compared across taxa with respect to the following parameters.

(1) Angle of lateral flexion at touchdown. Touchdown of the foot is an important event in the step cycle, as foot placement affects stride length. To evaluate the extent to which lateral spinal flexion brings the foot forward at touchdown, the angle of lateral flexion of the lumbar region at touchdown of the foot was compared across taxa. Values below 180° indicate flexion toward the ipsilateral foot (i.e., the spine is concave toward the foot that is in support), values above 180° indicate flexion toward the contralateral foot, and values of 180° indicate no flexion.

(2) Overall range of lateral flexion (difference between maximum angle of flexion and minimum angle of flexion). This parameter was calculated in order to reflect the overall range of motion in the lumbar region throughout the stride, rather than merely at touchdown. *L. tardigradus* and *N. coucang* were filmed for an earlier study which did not require full strides for analysis. To facilitate marker viewing, they were filmed closer to the camera than were the other taxa. As a result, only half-strides were available for analysis in the present

study. Therefore, the maximum/minimum angular difference was estimated for *L. tardigradus* and *N. coucang*: the average minimum flexion angle from support and swing phases was subtracted from the average maximum flexion angle from support and swing phases.

(3) BFD—bending footfall delay. This measurement, as calculated by Ritter (1996) for lizards, reflects the timing of maximum lateral flexion relative to touchdown of the ipsilateral foot (where the ipsilateral foot is on the side to which the back is flexed concavely). It is calculated as a percentage of stride duration:

$$BFD = [(T_{\max} - T_{td}) / Dur] \times 100$$

where T_{\max} is the time of maximum ipsilateral flexion, T_{td} is the time of ipsilateral touchdown, and Dur is the cycle duration.

A *BFD* of zero indicates that maximum lateral flexion coincides with ipsilateral touchdown. The more time elapsed between touchdown and maximum flexion, the higher the *BFD*. In this study, *BFD* was always positive, but since the stride is cyclical, it must be kept in mind that a *BFD* value of 100 is equivalent to a *BFD* of zero. Also, a *BFD* of 20, for example, would indicate that maximum flexion occurs at 20% of the stride duration *after* touchdown,

or that maximum flexion occurs at 80% of the stride duration *before* the next touchdown of the same foot (cf. Ritter, 1996, in which positive and negative values are reported to indicate maximum flexion occurring after or before touchdown, respectively).

Because the calculation of *BFD* requires a full stride, *Loris* and *N. coucang* are excluded from this part of the analysis (see above).

Statistical analysis

Values for the angular parameters and *BFD* were compared across taxa using ANOVA and unplanned comparisons among means, except in those cases in which the assumptions of ANOVA were not met and nonparametric tests were used (e.g., Kruskal–Wallis). The range of variation within each individual is represented by the value of each kinematic parameter across a number of strides. Therefore, sample sizes used for statistical tests correspond to number of strides measured for each individual (Table 1). Due to the small number of experimental subjects, and to avoid possible Type I error associated with inflated degrees of freedom, all individuals (even those within a species) were treated separately in statistical tests. In cases where individuals within a species were statistically indistinguishable, values were averaged only for the purposes of illustration (see Figures 3, 5, and 7). The angles and *BFD* values were also tested for correlation with body size and velocity using Kendall's coefficient of rank correlation (τ). Significance levels for all tests were set to $P \leq 0.05$.

Results

The values depicted in Figure 2 represent lateral movement of the lumbar spine during a single stride (touchdown of the foot to touchdown of the same foot) for each of the taxa walking at similar velocities. The taxa share a basic kinematic pattern. The lumbar

spine is at its most flexed toward the ipsilateral side (values below 180°) at or near touchdown of the foot. The spine then straightens out (approaches 180°) during support phase and begins to flex toward the contralateral side (values above 180°), reaching a peak at or near touchdown of the contralateral foot (C). After the ipsilateral foot is lifted at toeoff (TO), beginning swing phase, the spine straightens out again and begins to flex toward the ipsilateral side once more.

The parameters discussed below indicate to what extent the magnitude and timing of these spinal movements vary among the taxa, as well as how they are influenced by body size and changes in velocity.

Angle of lateral flexion at touchdown

Across taxa. Mean values of the angle of lateral flexion at touchdown across individuals [Table 3(a)] are significantly different (ANOVA; $F=9.78$, $df=8$, $P<0.001$). Based on a Games and Howell test for means with heterogeneous variances, individuals within the same species do not differ significantly from one another. In both species of *Nycticebus*, lateral flexion at touchdown is significantly more pronounced than in *Eulemur 2* and *Varecia 1*. The other taxa do not differ significantly from one another, but a general interspecific pattern is evident. In Figure 3(a), individuals within species are pooled for clarification, but the pattern is the same across individuals. That is, the most pronounced lateral flexion is used at touchdown by *Nycticebus* (both species), the least lateral flexion is used by the lemurids (*Varecia*, *Eulemur*), and the values for *Loris* and *Cheirogaleus* are intermediate.

The mean differences in flexion angle noted above do not take into consideration the effects of differences among the taxa in velocities sampled (Table 2), a potential confounding factor that can be controlled using analysis of covariance (ANCOVA)

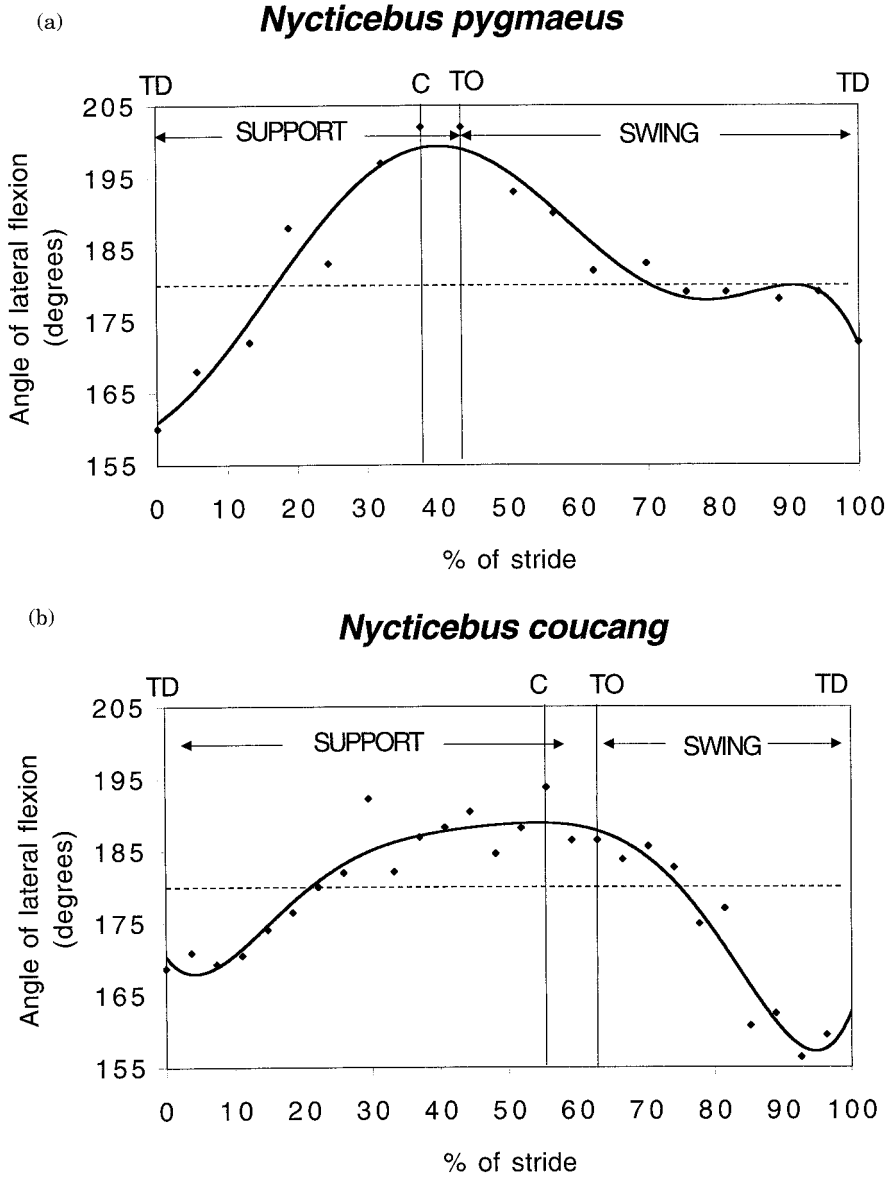


Figure 2. (a and b).

(Sokal & Rohlf, 1995). However, these data do not fit the assumptions of ANCOVA (e.g., the slopes of the regression lines of flexion angle on velocity are not parallel). As an alternative, the means were calculated and compared at similar velocities; i.e., at a velocity range common to all individuals

(51–75 cm/sec), but at reduced sample sizes. The means within this velocity range [Table 3(b)] are similar to those found when all velocities were included, and fall in the same rank order [Figure 3(b)]. Therefore, it appears that across all velocities, as well as at a given velocity, *Nycticebus* has the

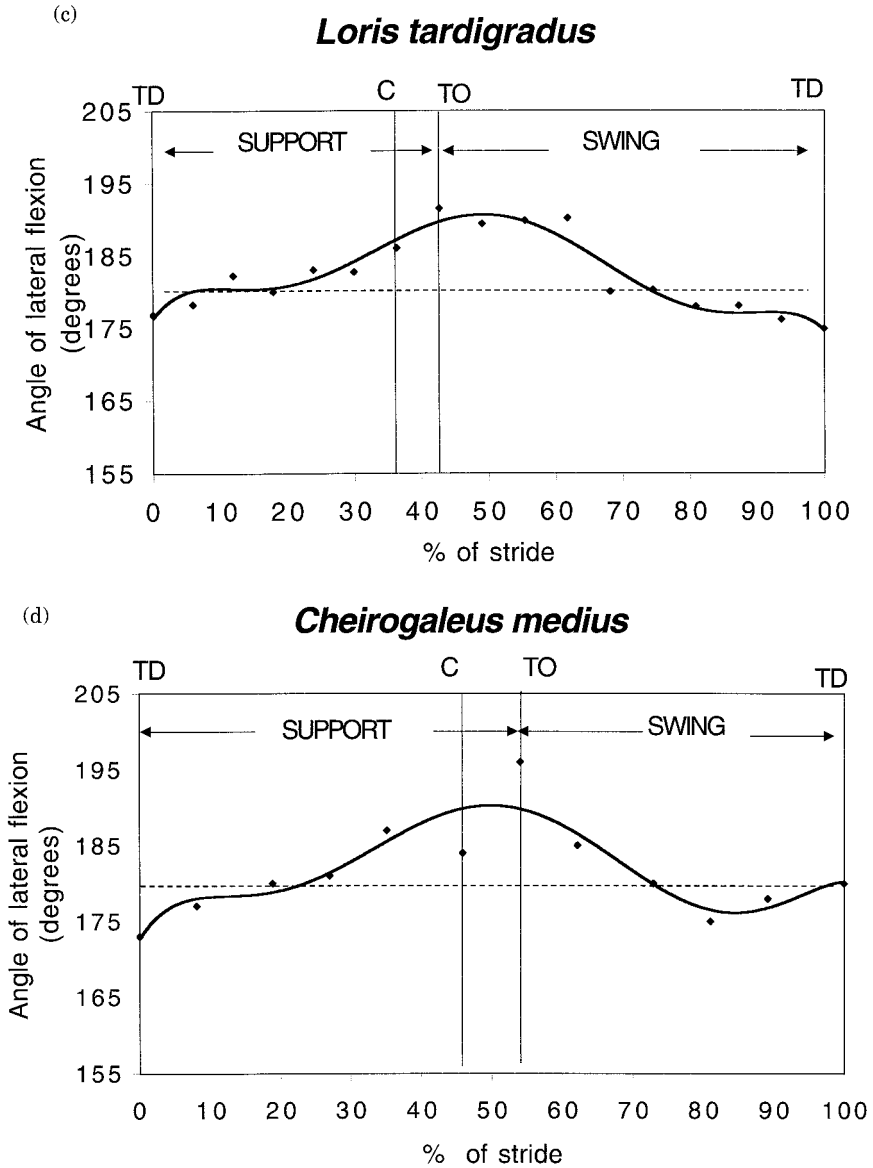


Figure 2. (c and d).

most pronounced lateral flexion at foot touchdown, and it is unlikely that differences among the taxa in velocity are confounding mean differences in flexion angle at touchdown.

Relationship with body size. There is no significant correlation between angle of lateral

flexion and body size (Kendall's tau=0.28, $P>0.10$), as the taxa with the smallest angles (*N. coucang* and *N. pygmaeus*) are neither the smallest nor the largest in body size [Figure 3(a)].

Relationship with velocity. When all taxa are combined (either by all individuals or by

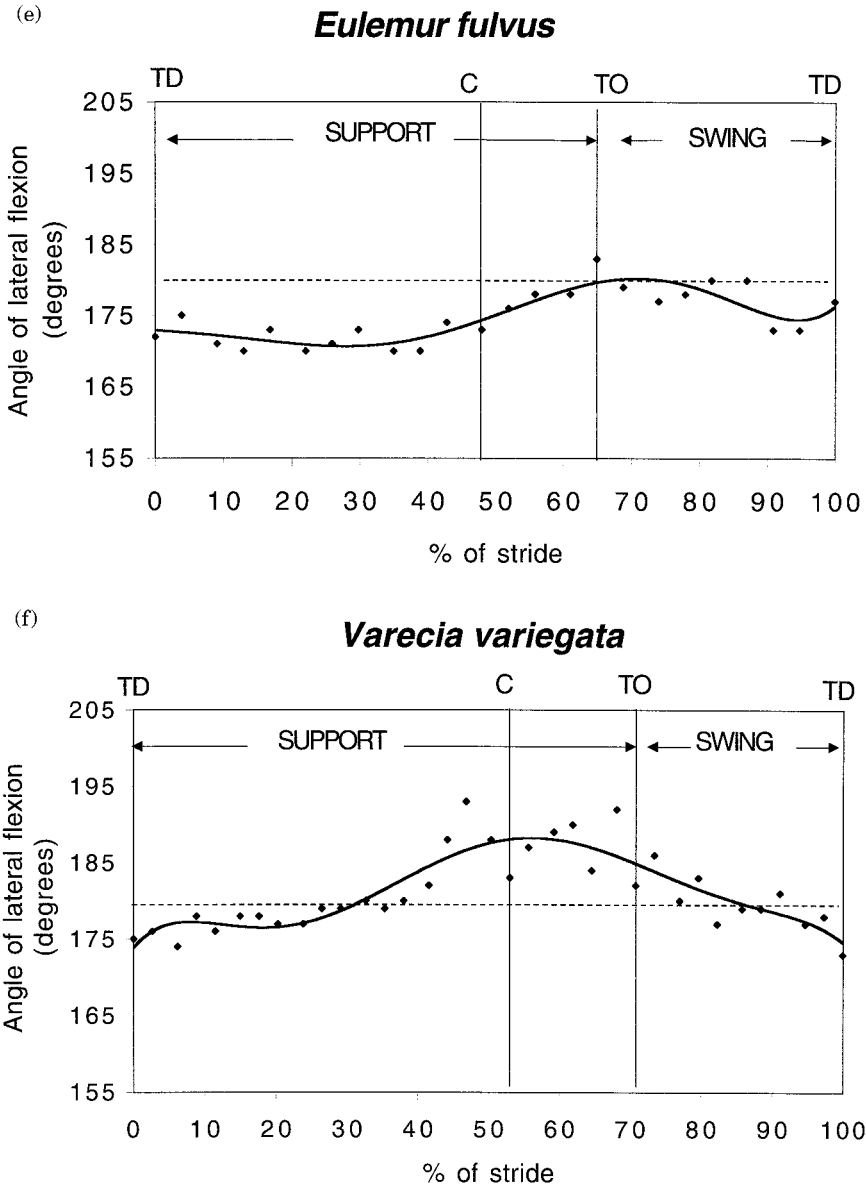


Figure 2. (e and f).

Figure 2. Changes in the angle of lateral flexion of the lumbar region during a single representative stride for each of the taxa (a-f) walking at similar velocities (range 46–62 cm/sec). The x axis represents time as a percentage of stride duration. The curved line on each graph is a sixth order polynomial, plotted for visual purposes only. The dashed line represents 180°. TD=touchdown of the ipsilateral foot, C=touchdown of the contralateral foot, TO=toeoff of the ipsilateral foot. Values below 180° indicate spinal flexion toward the ipsilateral foot; values above 180° indicate spinal flexion toward the contralateral foot.

Table 3(a) Means, standard deviations, and sample sizes for data in Figures 3(a), 5(a) and 7(a)

Species	Angle at touchdown			Overall flexion			BFD		
	Mean	S.D.	N	Mean	S.D.	N	Mean	S.D.	N
<i>Cheirogaleus medius</i> (pooled)	173	6.2	81	23	5.1	100	5.0	6.4	100
<i>Cheirogaleus medius</i> 1	174	4.3	53	22	5.0	72	3.8	5.9	72
<i>Cheirogaleus medius</i> 2	172	8.6	28	26	3.5	28	8.2	6.8	28
<i>Eulemur fulvus</i> (pooled)	177	5.2	57	17	3.1	59	9.9	9.6	59
<i>Eulemur fulvus</i> 1	176	3.6	24	18	2.5	24	6.7	5.9	24
<i>Eulemur fulvus</i> 2	178	6.0	33	16	3.1	35	12.2	11.0	35
<i>Varecia variegata</i> (pooled)	177	4.0	61	21	3.5	61	11.0	6.9	61
<i>Varecia variegata</i> 1	178	3.8	37	20	3.5	37	11.9	7.6	37
<i>Varecia variegata</i> 2	175	3.7	24	22	3.4	24	9.8	5.5	24
<i>Nycticebus pygmaeus</i>	169	5.9	18	37	4.8	18	6.7	8.3	18
<i>Nycticebus coucang</i>	168	5.6	12	25	4.0	12	—	—	—
<i>Loris tardigradus</i>	175	2.7	11	15	4.5	11	—	—	—

Table 3(b) Means, standard deviations, and sample sizes for data in Figures 3(b), 5(b) and 7(b) (velocity range 51–75 cm/s)

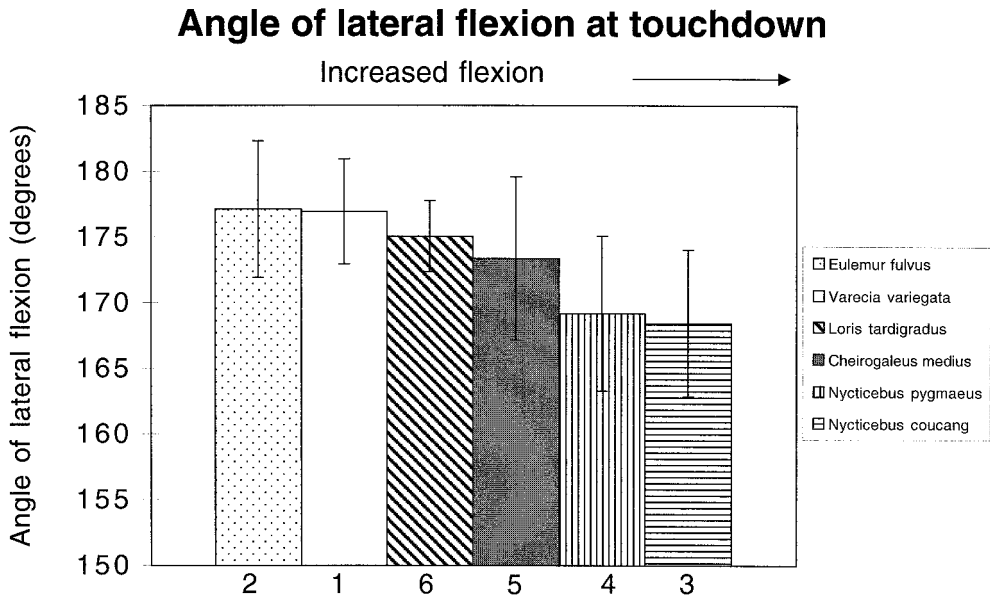
Species	Angle at touchdown			Overall flexion			BFD		
	Mean	S.D.	N	Mean	S.D.	N	Mean	S.D.	N
<i>Cheirogaleus medius</i> (pooled)	172	5.8	15	24	3.8	22	2.6	3.8	22
<i>Cheirogaleus medius</i> 1	172	3.1	10	22	3.1	17	2.9	3.9	17
<i>Cheirogaleus medius</i> 2	171	9.8	5	27	4.1	5	1.5	3.4	5
<i>Eulemur fulvus</i> (pooled)	178	5.1	27	16	3.6	27	12.2	10.3	27
<i>Eulemur fulvus</i> 1	177	2.9	9	19	2.8	9	7.4	6.4	9
<i>Eulemur fulvus</i> 2	178	5.9	18	15	3.4	18	14.6	11.2	18
<i>Varecia variegata</i> (pooled)	179	3.8	24	20	2.9	24	12.7	0.3	24
<i>Varecia variegata</i> 1	179	3.9	21	20	3.0	21	12.5	8.8	21
<i>Varecia variegata</i> 2	178	2.9	3	22	1	3	14.1	3.0	3
<i>Nycticebus pygmaeus</i>	166	3.4	7	37	2.7	7	1.8	3.1	7
<i>Nycticebus coucang</i>	162	0.7	2	32	2.1	2	—	—	—
<i>Loris tardigradus</i>	176	1.4	2	13	5.7	2	—	—	—

species means), the angle of lateral flexion at touchdown is not correlated with velocity. However, there is a significant negative correlation between flexion angle at touchdown and velocity among the lorids [Figure 4(a), Table 4], driven by the values for *N. pygmaeus* [Figure 4(b); *Loris* and *N. coucang* show no correlation individually]. In other words, for *N. pygmaeus* in particular, lateral flexion at touchdown becomes more pronounced at higher velocities. By contrast, the other taxa exhibit either no correlation (*Cheirogaleus* 2, *Eulemur* 1) or a significant

positive correlation [*Cheirogaleus* 1, *Eulemur* 2; Figures 4(c) and (d), Table 4]. Although the combined values for the two *Varecia* individuals exhibit a significant negative correlation, this is probably spurious, as neither individual exhibits a significant correlation (Table 4).

The range of velocities sampled differs across taxa and individuals (Table 2). This could potentially affect the results reported above regarding correlation of flexion angle at touchdown with velocity. For example, *Cheirogaleus* 1 walked at a wider range of

(a)



(b)

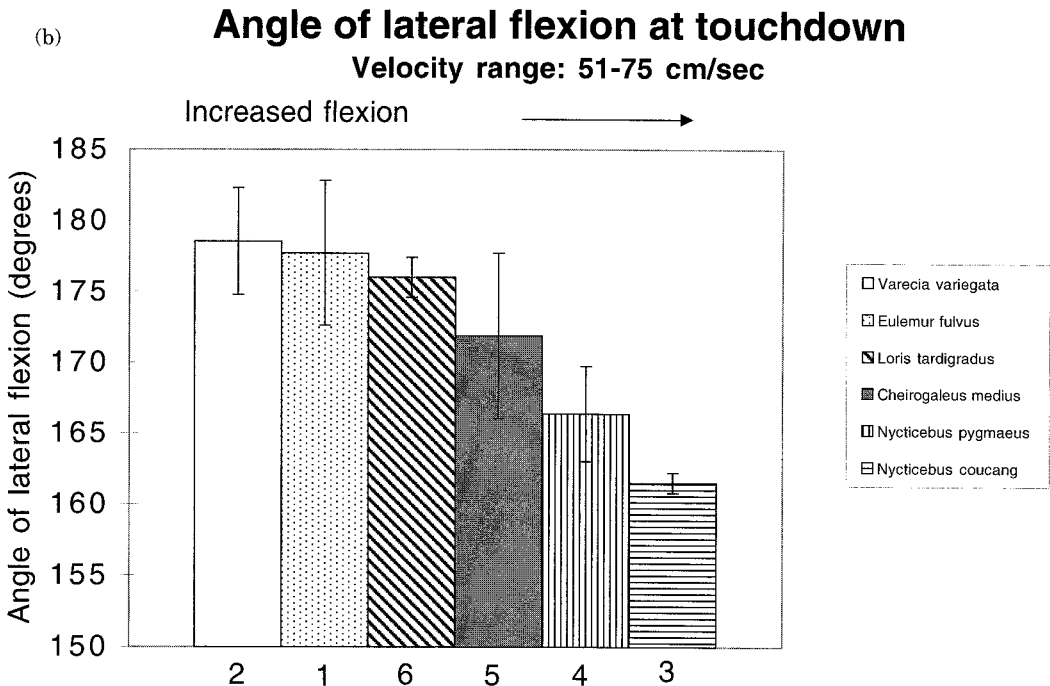


Figure 3. (a) Means plus or minus one standard deviation for angle of lateral flexion at ipsilateral foot touchdown with all velocities combined; (b) angle of lateral flexion at ipsilateral foot touchdown at velocity range 51–75 cm/sec (reduced sample sizes). Numbers listed on the x axis represent body size ranks, where 1 is the largest. Means for *Cheirogaleus*, *Eulemur* and *Varecia* represent pooled individuals, which do not differ significantly from one another. Distribution of values is similar for separate individuals—see text for further discussion. See Table 3(a) and (b) for means, standard deviations and sample sizes.

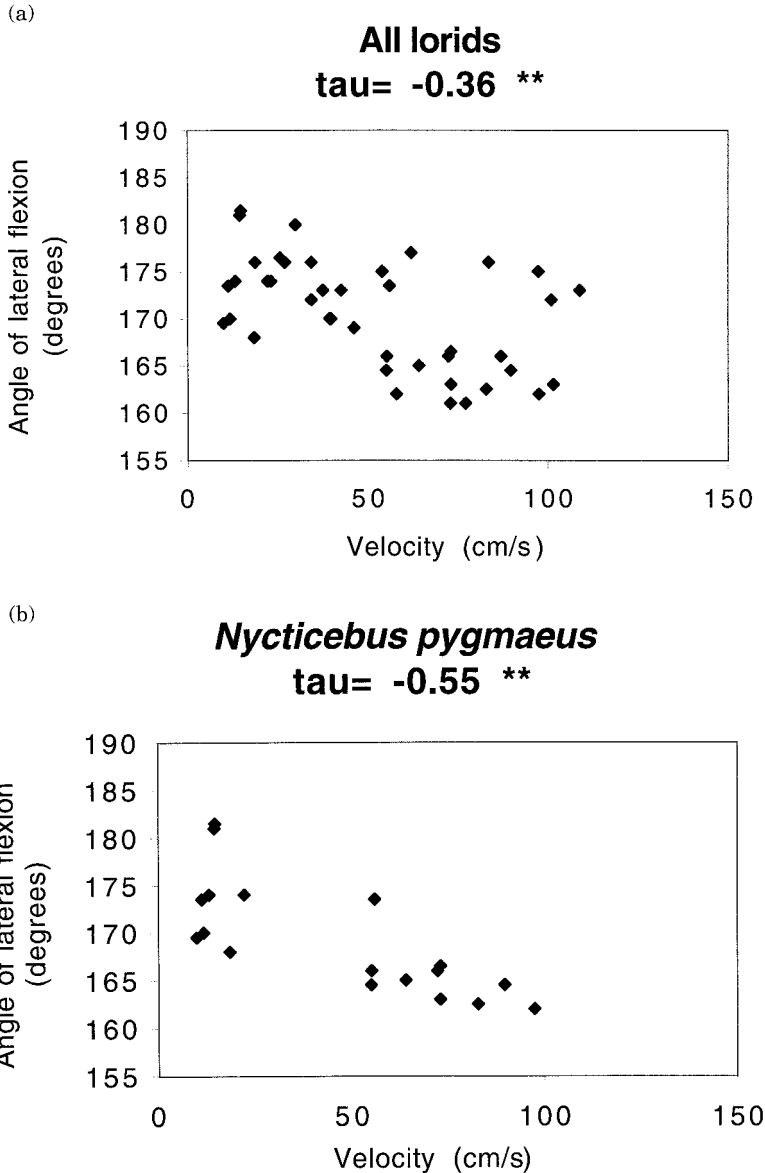


Figure 4. (a and b).

velocities than did *Cheirogaleus 2*, and only *Cheirogaleus 1* exhibits a significant correlation with velocity. Similarly, the only loricid with a significant correlation between velocity and angle at touchdown was *Nycticebus pygmaeus*, which also walked at the widest range of velocities (but not

necessarily the highest maximum velocity) among the lorids. It is possible then, that resampling *Cheirogaleus 2*, *N. coucang*, and *L. tardigradus* at additional velocities would result in stronger correlations. On the other hand, *Eulemur 2* exhibits a significant correlation, but was sampled at a slightly

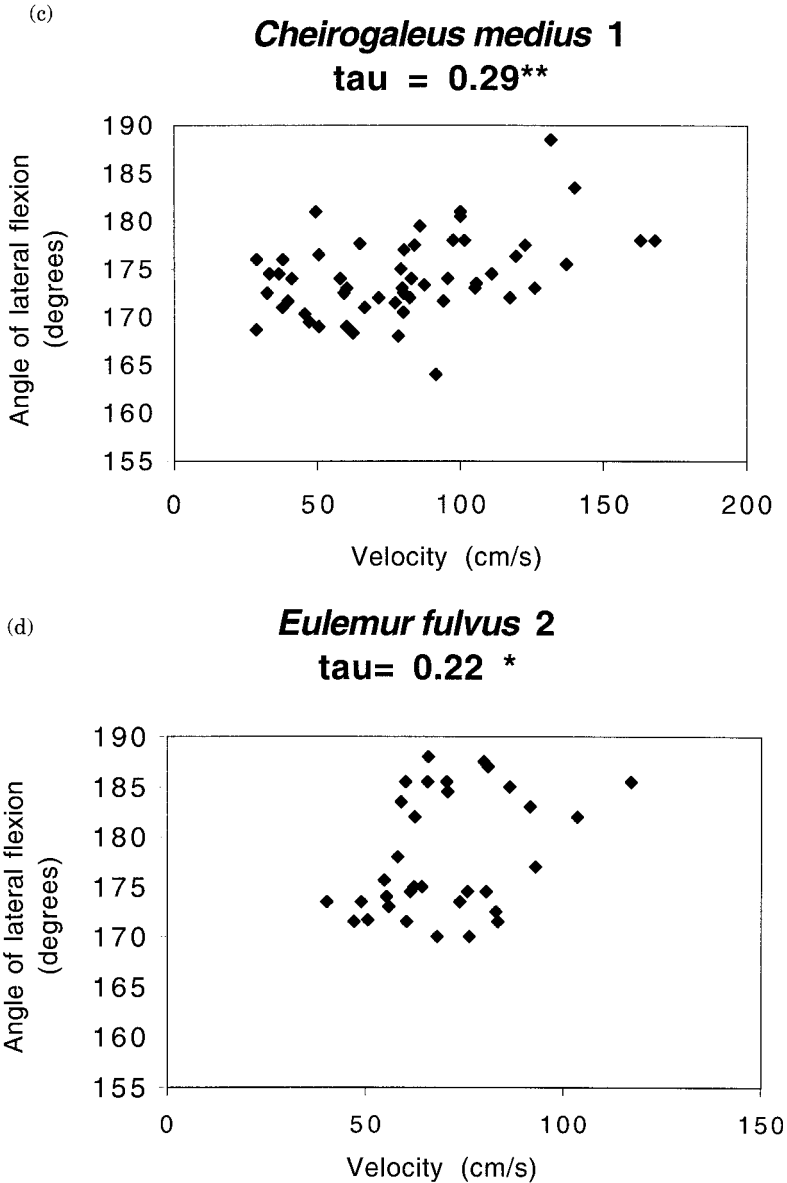


Figure 4. (c and d).

Figure 4. Kendall's coefficient of rank correlation between angle of lateral flexion at ipsilateral foot touchdown and velocity in (a) all lorids, (b) *Nycticebus pygmaeus*, (c) *Cheirogaleus medius* 1, and (d) *Eulemur fulvus* 2. ** $P \leq 0.01$, * $P \leq 0.05$. See Table 4.

narrower range of velocities than *Eulemur* 1, which shows no correlation. There are also differences in the ranges of velocities sampled for the two *Varecia* individuals, but

neither shows a significant correlation with velocity. Therefore, at least for *Eulemur* and *Varecia*, velocity range does not appear to directly influence the correlation analysis.

Table 4 Kendall's coefficient of rank correlation between velocity and both magnitude and timing of lateral spinal flexion

Species	Velocity vs. angle at touchdown	Velocity vs. overall flexion	Velocity vs. BFD
<i>Cheirogaleus</i> 1	0.29*	-0.45*	-0.26*
<i>Cheirogaleus</i> 2	ns	0.28†	ns
<i>Cheirogaleus</i> pooled	0.15†	-0.43*	-0.33*
<i>Eulemur</i> 1	ns	ns	ns
<i>Eulemur</i> 2	0.22†	ns	ns
<i>Eulemur</i> pooled	ns	ns	ns
<i>Varecia</i> 1	ns	ns	ns
<i>Varecia</i> 2	ns	ns	-0.36*
<i>Varecia</i> pooled	-0.24†	ns	-0.15†
<i>Loris</i>	ns	ns	n/a
<i>Nycticebus coucang</i>	ns	ns	n/a
<i>Nycticebus pygmaeus</i>	-0.55*	0.35†	-0.55*
All lorids	-0.36*	ns	n/a
All taxa (individuals)	ns	-0.23*	-0.14*
All taxa (species means)	ns	ns	ns

* $P \leq 0.01$.† $P \leq 0.05$.

Alternatively, differences across taxa with respect to correlation with velocity may be influenced by differences in sample size among the taxa (Table 1).

Overall range of lateral flexion (differences between maximum angle of flexion and minimum angle of flexion)

Across taxa. A nonparametric Kruskal–Wallis test ($H=135.76$, $df=8$, $P<0.001$), in conjunction with a Games and Howell test, was used to test for differences across all taxa and for pairwise comparisons. Individuals within species do not differ significantly from one another, with the exception of individuals of *Cheirogaleus*. The most notable result is that *N. pygmaeus* exhibits a significantly greater range of lateral flexion throughout the stride than do all other taxa, whether means are compared across individuals or species [Figure 5(a), Table 3(a)]. The separation of values among the three lorids (*N. pygmaeus*, *N. coucang*, and *L. tardigradus*) is surprising. However, as discussed above, the values for *N. coucang* and *Loris* are estimated based on half-strides

and their values for this parameter may not be fully reliable.

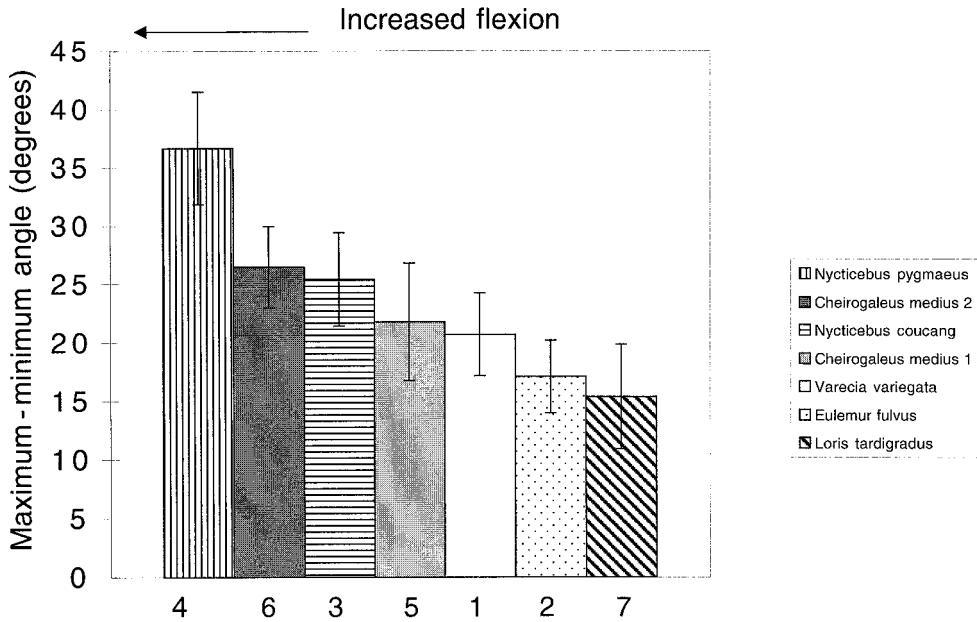
As noted above for flexion angle at foot touchdown, similar results were found when means for overall flexion were compared at a similar velocity range [Table 3(b)]. One exception is that the rank order of *N. coucang* and *C. medius* 2 are transposed [Figure 5(b)]. Nevertheless, it is unlikely that velocity differences among the taxa are confounding mean differences in overall lateral flexion.

Relationship with body size. There is no significant correlation between overall range of flexion and body size (Kendall's tau = -0.11, $P>0.10$).

Relationship with velocity. There is a significantly negative correlation between overall range of lateral flexion and velocity across all individuals, but no correlation when species means are used. When individuals are examined, separately, only *N. pygmaeus* and *C. medius* (both individuals) exhibit significant correlations (Table 4). For

(a)

Overall range of flexion



(b)

Overall range of flexion

Velocity range 51-75 cm/s

← Increased flexion

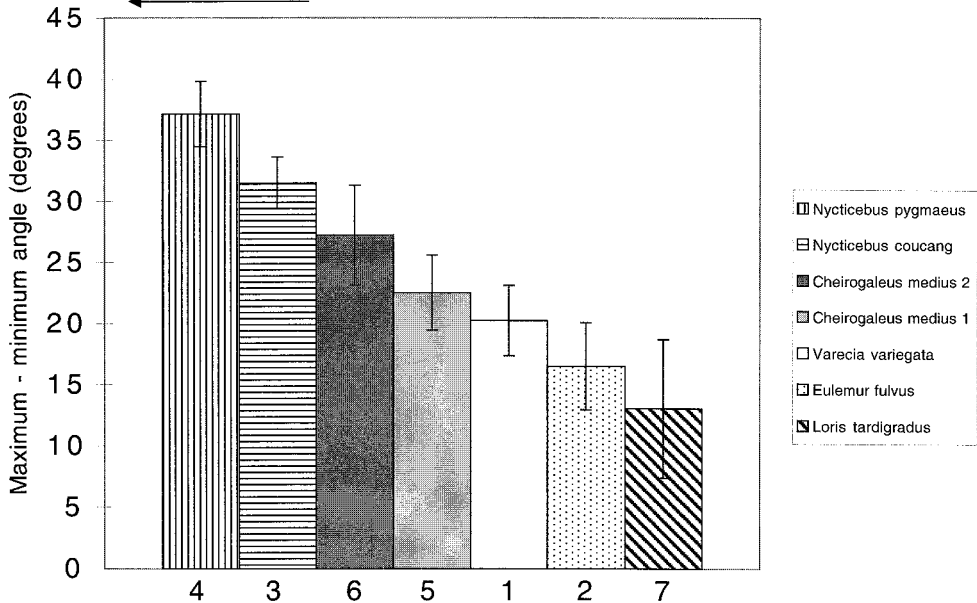


Figure 5. (a) Means plus or minus one standard deviation for overall range of lateral flexion with all velocities combined; (b) overall range of lateral flexion at velocity range 51–75 cm/sec (reduced sample sizes). Numbers listed on the x axis represent body size ranks, where 1 is the largest. Means for *Eulemur* and *Varecia* represent pooled individuals, which do not differ significantly from one another. Distribution of values is similar for separate individuals—see text for further discussion. See Table 3(a) and (b) for means, standard deviations, and sample sizes.

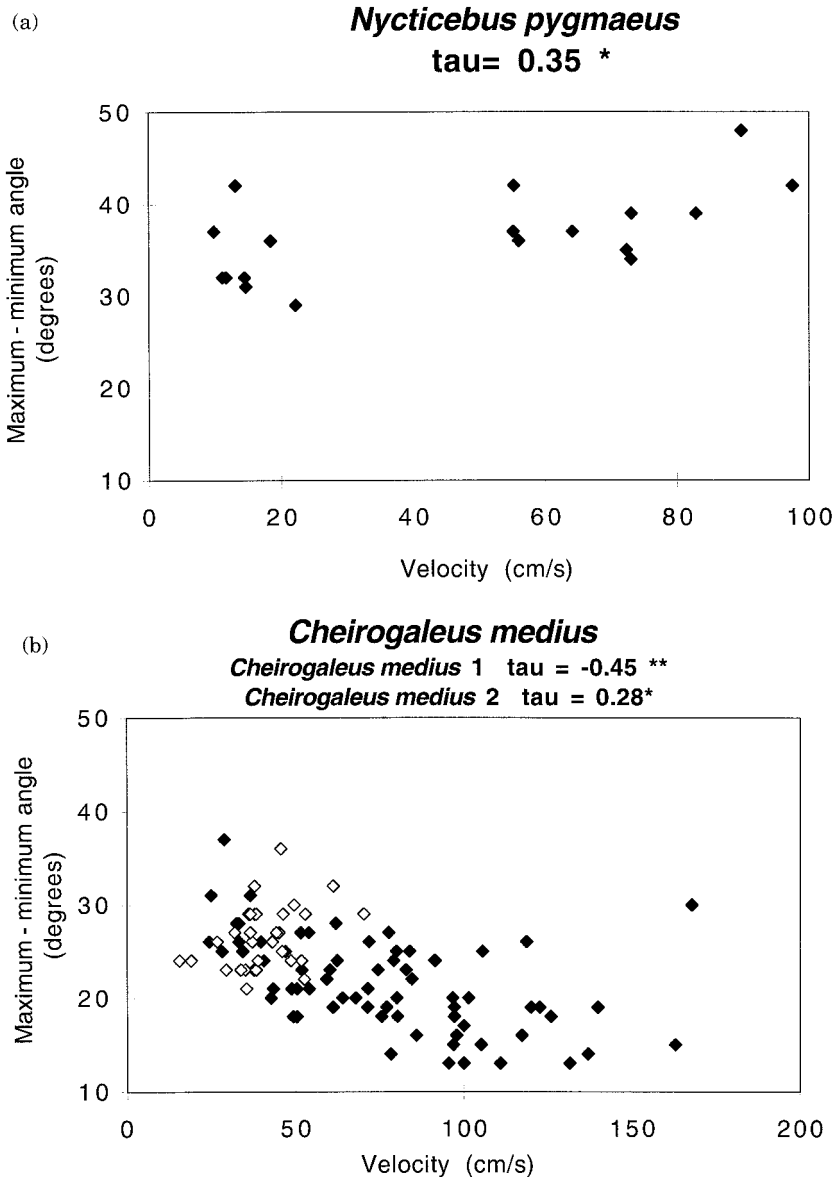


Figure 6. Kendall's coefficient of rank correlation between overall range of lateral flexion and velocity in (a) *Nycticebus pygmaeus* and (b) *Cheirogaleus medius* (closed diamonds represent *C. medius* 1; open diamonds represent *C. medius* 2). ** $P \leq 0.01$, * $P \leq 0.05$. See Table 4.

N. pygmaeus, the correlation is positive [Figure 6(a)], indicating that overall flexion becomes more pronounced as velocity increases. By contrast, the correlation is negative in *C. medius* 1 [Figure 6(b)], indicating that overall flexion decreases as

velocity increases. The contrast between *N. pygmaeus* and *C. medius* 1 resembles their contrasting pattern with respect to the relationship between velocity and flexion angle at touchdown [Figure 4(b) and (c)]. However, results for *C. medius* 2 weaken this

comparison. *Cheirogaleus 2* exhibits a significantly positive correlation of overall flexion with velocity, and shows no correlation of velocity and flexion angle at touchdown.

It is unlikely that differences among the taxa in range of velocities sampled has influenced the correlation analysis because (1) both cheirogaleids exhibit significant correlations despite a prominent difference in their velocity ranges (Table 2), and (2) none of the *Eulemur* or *Varecia* individuals exhibits significant correlations despite differences in velocity ranges (Table 2).

Bending-footfall delay

Across taxa. Bending-footfall delay could not be calculated for *L. tardigradus* and *N. coucang* because only half-strides were filmed for these two taxa. A nonparametric Kruskal–Wallis test ($H=44.14$, $df=6$, $P<0.001$) in conjunction with a Games and Howell test was used to test for differences across all other taxa and for pairwise comparisons.

With all velocities considered together, the *BFD* value is greater than zero on average for all of the taxa. That is, for all taxa, maximum spinal flexion does not on average coincide with touchdown of the ipsilateral foot, but occurs up to an average of 12% of the stride duration after foot touchdown [Table 3(a)].

Individuals within the same species do not differ significantly from one another, although their values are more disparate than the angular values discussed above [Table 3(a), Figure 7(a)]. *Cheirogaleus 1* differs significantly from *Varecia* (both individuals), which was the only significant interspecific difference found, according to a Games and Howell test for means with heterogeneous variances ($P\leq 0.05$). Lack of statistical significance among the other taxa is not surprising, given the large standard deviations of the *BFD* means [Table 3(a)]. Individuals within species were not pooled

in Figure 7(a), in order to reflect their divergent *BFD* values. The variation in *BFD* does not appear to show any relation to locomotor pattern (or body size; see below) since *N. pygmaeus*, the most specialized primate of the sample with respect to back movement, does not differ significantly from the other taxa.

When means are compared to a similar velocity range [Figure 7(b), Table 3(b)], the distribution of values is quite dissimilar from that depicted in Figure 7(a), suggesting that velocity differences among the individuals make interspecific comparisons of *BFD* unreliable. Nevertheless, velocity differences aside, the *BFD* values for these strepsirhines as a group are revealing when compared to those of other vertebrates (see Discussion).

Relationship with body size. There is no significant correlation between body size and *BFD* (Kendall's tau = 0.33, $P>0.10$).

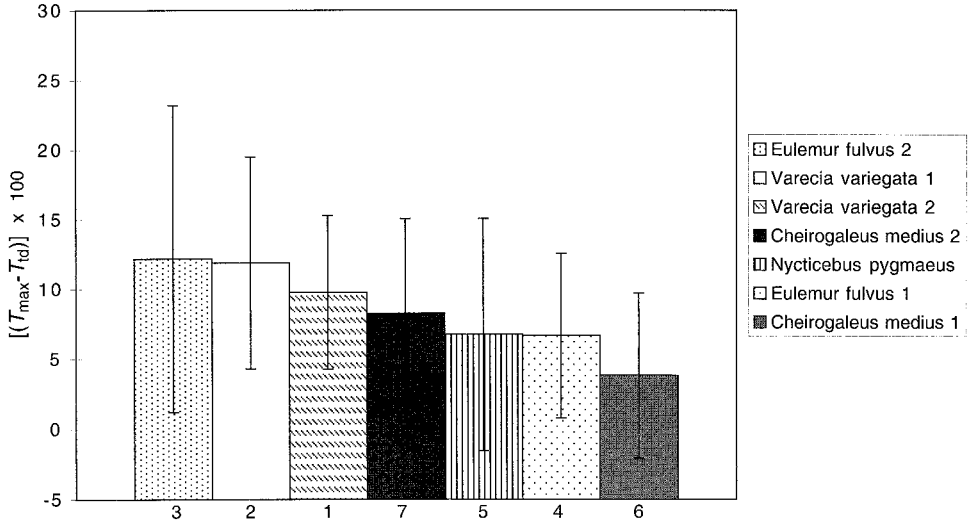
Relationship with velocity. Among all individuals, there is a significant negative correlation between velocity and bending-footfall delay [Figure 8(a), Table 4]. In other words, as velocity increases, maximum lateral flexion occurs closer in time to ipsilateral touchdown. There is no correlation when species means are used. When individuals are examined separately, *N. pygmaeus*, *C. medius 1*, and *V. variegata 2* exhibit significant negative correlations (Figure 8), and all other individuals (*E. fulvus 1* and 2, *C. medius 2*, *V. variegata 1*) show no correlation. The results for all taxa are summarized in Table 4.

Discussion

An emphasis on sagittal flexion and extension of the spine is a well known trait that distinguishes mammals from other vertebrates (e.g., Wake, 1979). Nevertheless, there is more complexity (both functionally and taxonomically) to spinal locomotor

(a)

Bending-footfall delay



(b)

**Bending-footfall delay
Velocity range 51-75 cm/s**

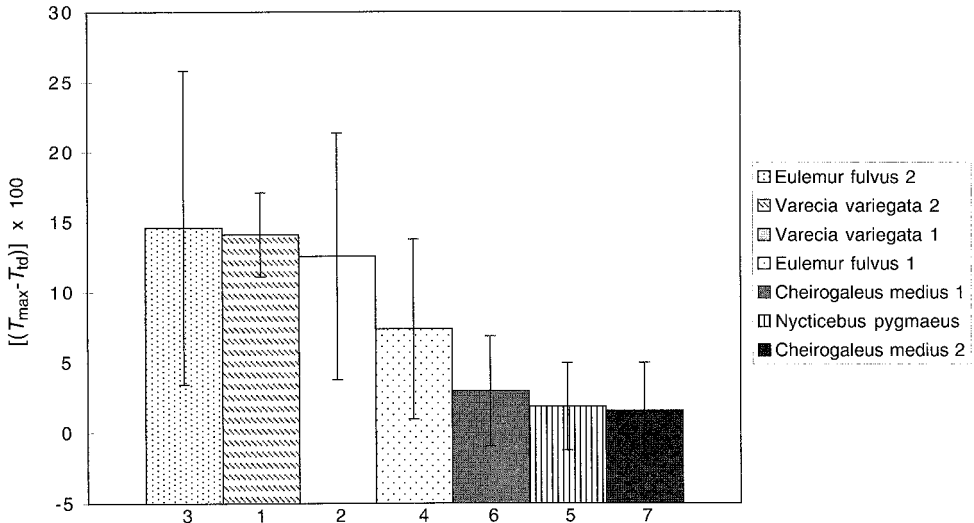


Figure 7. Means plus or minus one standard deviation for (a) bending-footfall delay with all velocities combined; (b) for bending-footfall delay at velocity range 51–75 cm/sec (reduced sample sizes). Numbers listed on the x axis represent body size ranks, where 1 is the largest. Individuals within species do not differ significantly from one another, but their means are not pooled in order to reflect their divergent values. See Table 3(a) and (b) for means, standard deviations and sample sizes.

function than is expressed by a single mammal–nonmammal dichotomy. For example, the few studies that have addressed lateral spinal bending in mammals (e.g., Carlson *et al.*, 1979; Pridmore, 1992) point to its continued importance in mammalian locomotion. In addition, although both amphibians and reptiles emphasize lateral spinal flexion during locomotion, the biomechanical role of trunk movements differs between the two groups, as well as across species within groups (Ritter, 1992, 1995, 1996). In fact, Ritter (1995, 1996) has effectively demonstrated that with respect to several parameters (e.g., back muscle function, spinal kinematics), spinal locomotor function in lizards more closely resembles that of mammals than that of amphibians (and see Brainerd, 1999 regarding trunk musculature and breathing mechanisms in tetrapods). Consequently, Ritter (1995) has proposed that features such as a reduction in degree of lateral flexion at faster speeds and an emphasis on spinal stability may be a synapomorphy of amniotes.

The results from this study are illuminating in the context of the complex issues surrounding spinal function in tetrapod locomotion. First, the strepsirhine data have confirmed that lateral spinal bending continues to be a functional component of mammalian quadrupedal walking. That is, the strepsirhines share with each other and with quadrupedal tetrapods in general, a basic spinal kinematic pattern during a walking stride, in which the spine bends from side to side as each foot swings forward and then begins support phase. This study, based on flexion at the lumbosacral joint, indicates that the amount of deviation across the six species ranges on average from 8–18° to either side. The amount of deviation is not dissimilar to values of lateral flexion reported for other taxa, but those values are not necessarily directly comparable to ours because they were based on different anatomical landmarks. For example, Carlson

et al. (1979) reported 10–15° of lateral flexion in cats, based on the angle between the ninth thoracic vertebra and the fifth lumbar vertebra, with the third lumbar vertebra as the vertex. Ritter (1996) found a range of 10–25° of lateral flexion in lizards, based on a “mid-trunk” angle. By contrast, Demes *et al.* (1990) reported a considerably larger angle of lateral flexion for *L. tardigradus* (50°). This value was not measured directly from movement of spinal markers, but was calculated as the amount of lumbar lateral flexion required to account for the difference between observed stride length and predicted stride length assuming pendular movement of the hindlimb. It was also based on flexion around the center of the lumbar region, which might account for the notable difference from the values for *Loris* reported here.

Second, and most important, this study’s comparative sample has demonstrated that there is interspecific variation in the means by which strepsirhines use lateral spinal flexion during the walking cycle with respect to magnitude and changes with velocity. In addition, the timing of lateral flexion in strepsirhines appears to differ from that reported for lizards. Thus, just as there is variation among reptiles and between reptiles and amphibians, there may not be a “mammalian” spinal kinematic pattern *per se*. Rather, it appears that spinal kinematics in tetrapods varies both within and between groups, as discussed below.

Magnitude of lateral bending

A notable result is the distinction of *Nycticebus* (especially *N. pygmaeus*) with respect to *Loris* as well as to the non-lorid taxa. *N. pygmaeus* uses more lateral flexion overall than do all other taxa, and both species of *Nycticebus* use more lateral flexion at touchdown than do all other taxa. Interestingly, *Loris* is more similar to *Cheirogaleus*, *Eulemur* and *Varecia* than it is

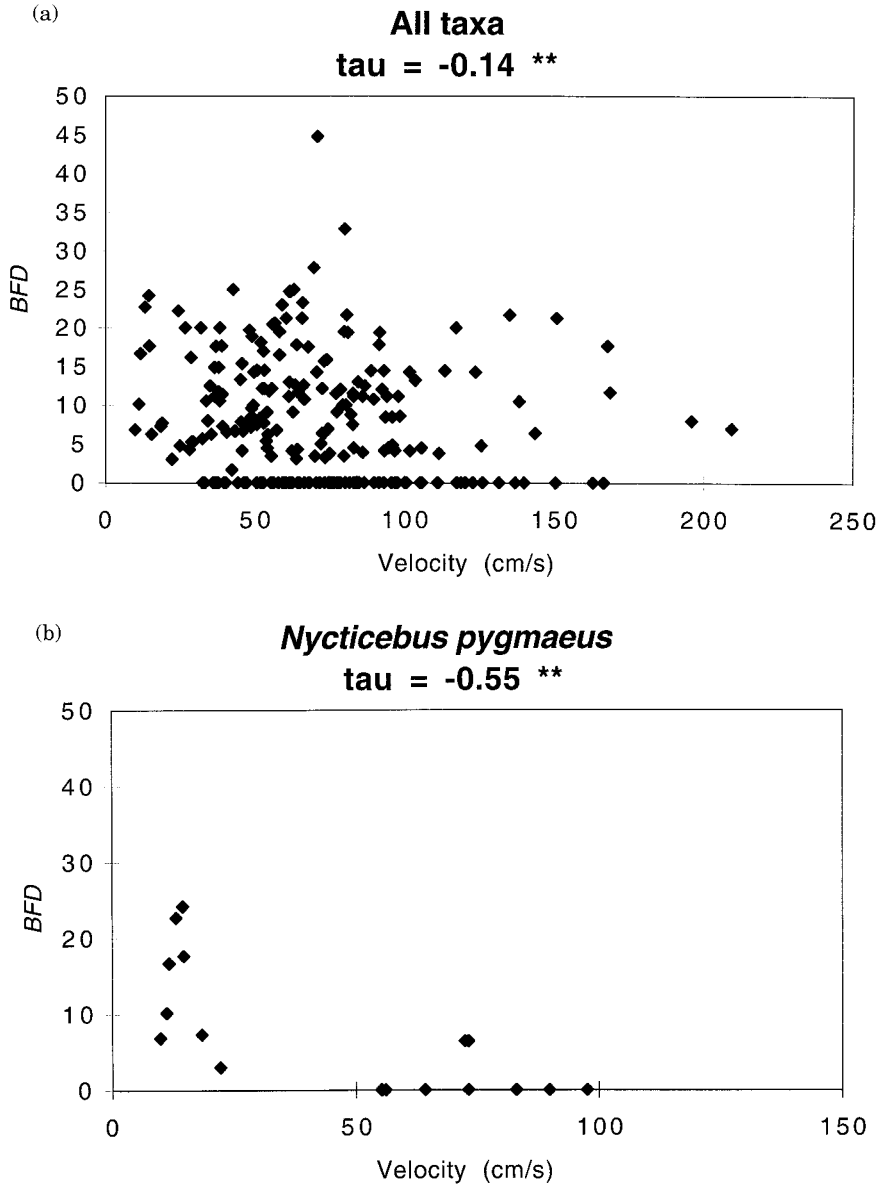


Figure 8. (a and b).

to *Nycticebus* with respect to the angle of lateral flexion at touchdown, and *Loris* is distinct from *Nycticebus* with respect to overall range of lateral flexion (although values for *Loris*' and *N. coucang*'s range of flexion are treated with caution because they are estimates). It appears that *Nycticebus* is

unique among these strepsirhines, and that within the lorids there are clear distinctions between *Nycticebus* (especially, *N. pygmaeus*) and *Loris*. Morphological correlates to these distinctions are discussed below.

The distinction between *N. pygmaeus* and *N. coucang* in overall range of flexion is

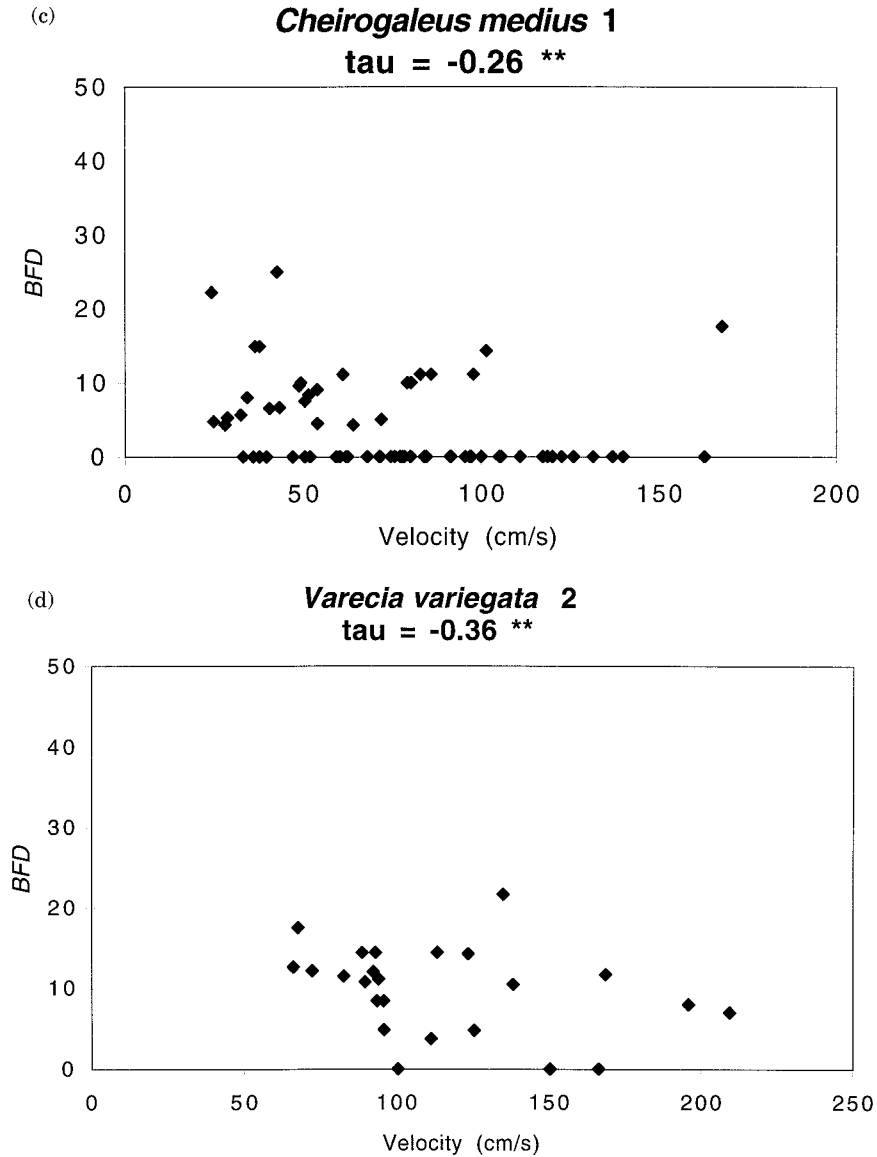


Figure 8. (c and d).

Figure 8. Kendall's coefficient of rank correlation between bending-footfall delay and velocity among (a) all taxa, (b) *Nycticebus pygmaeus*, (c) *Cheirogaleus medius* 1, and (d) *Varecia variegata* 2. ** $P \leq 0.01$. See Table 4.

perplexing, given their similarity in flexion angle at touchdown. As discussed above, the values for *N. coucang* for overall flexion are treated with caution, as they are based on half-strides. However, research by others

has demonstrated that *N. coucang* and *N. pygmaeus* are divergent in some morphological features (Gomez, 1992; Ravosa, 1998), so the kinematic differences observed here may be noteworthy. Further research

comparing *N. coucang* and *N. pygmaeus* is necessary to confirm the differences.

Another factor that might contribute to the differences among the taxa in lateral spinal bending is the size of the support. The "fine branch niche" has been noted to be an important element in the origin of primates (Cartmill, 1972, 1992; Sussman, 1991). If quadrupedal locomotion on small branches requires more lateral spinal bending than locomotion on larger branches, lateral bending might have been an important anatomical adaptation in the early evolution of primates. In this study, the smaller taxa (*Cheirogaleus*, *Loris*, *Nycticebus*) were tested on a pole of 3 cm diameter, and the larger taxa (*Eulemur*, *Varecia*) walked on a 5 cm pole. These pole sizes were chosen as reasonable substitutes for branch sizes that might be utilized by these taxa in their natural environments, but were not designed to test hypotheses regarding relative size or orientation of substrates. Nevertheless, differences exhibited by the three smaller taxa on a similar sized pole are suggestive of more than an influence of substrate. Future research would benefit from a closer examination of the effects of substrate size and orientation on spinal kinematics, especially given its potential relevance to questions of primate origins and evolution.

It should also be noted that in this study, lateral flexion was measured at the lumbosacral joint, which does not reflect lateral flexion *within* the lumbar region. A comparison of lateral flexion within the lumbar region might have revealed patterns different from those reported here, but such a parameter is more difficult to measure due to the relatively small body size of these taxa. In addition, it would have been beneficial to evaluate the functional relationship between movement in the thoracic *vs.* lumbar regions, but skin movement prevented us from reliably placing markers in the thoracic region.

Timing of lateral bending

Maximum lateral bending did not (on average) coincide with touchdown of the ipsilateral foot in any of the taxa. Rather, the average *BFD* values were all greater than zero, indicating that maximum bending occurred up to an average of 12% *after* touchdown (range of 0–45%). *N. pygmaeus* (the only lorid available for this part of the study) does not differ significantly from the other taxa with respect to the timing of lateral bending relative to foot touchdown.

The *BFD* data for strepsirhines are interesting in light of similar data reported for lizards, although as noted above, *BFD* values reported for lizards were based on a measurement of lateral flexion at mid-trunk (Ritter, 1996), not at the lumbosacral joint. In both strepsirhines and lizards, maximum lateral flexion does not always coincide with touchdown. However, whereas in strepsirhines maximum lateral flexion occurs between 0 and 45% of the stride *after* touchdown, in lizards, it occurs between 0 and 40% of the stride *before* touchdown (Ritter, 1995, 1996). These ranges represent different portions of the stride cycle—i.e., maximum flexion occurs on average during support phase in strepsirhines, and during swing phase in lizards.

The timing differences between these two groups can possibly be explained in relation to their differences in gait (footfall sequence). Lizards use a lateral sequence walking gait (LH–LF–RH–RF, where L, R are left, right, and H, F are hindlimb, forelimb) or a walking trot (diagonal forelimb and hindlimb swing and land in unison) (Hildebrand, 1976). In both types of gaits, spinal flexion toward the swinging hindlimb (ipsilateral concavity) brings the foot further forward, increasing stride length. During ipsilateral hindlimb swing phase, the contralateral forelimb and hindlimb are widely spaced apart, so spinal flexion toward the ipsilateral side (which produces contralateral convexity) is compatible with their

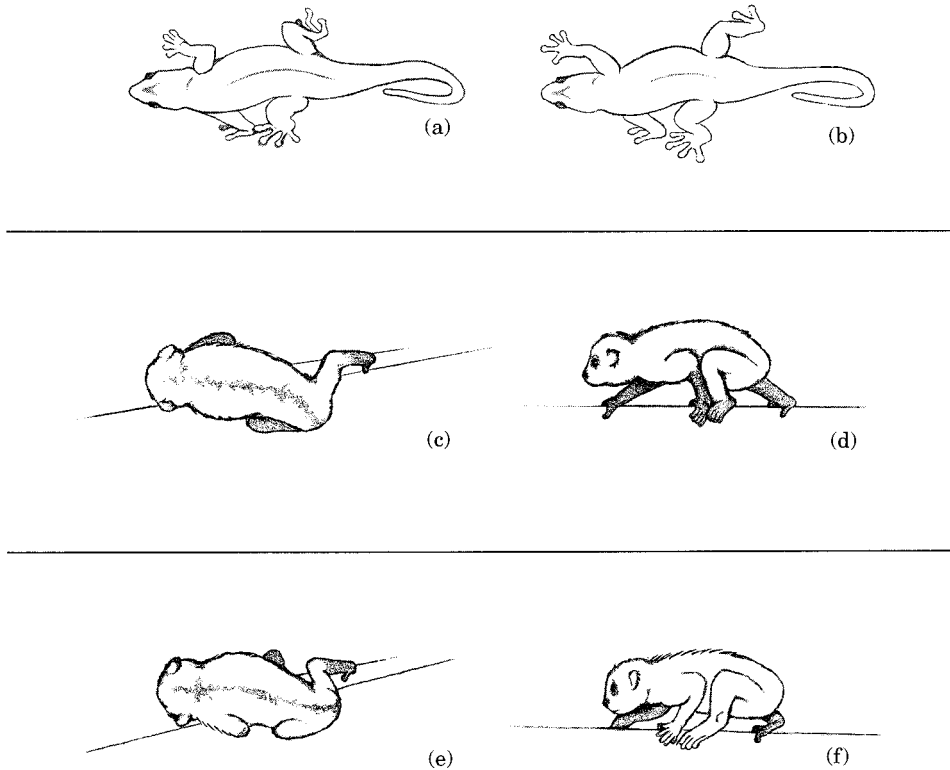


Figure 9. Positions of the forelimbs and hindlimbs: (a) late swing phase of the left foot (just before touchdown) in a lizard walking with a lateral sequence gait (overhead view); (b) late swing phase of the left foot (just before touchdown) in a lizard using a walking trot (overhead view); (c) support phase of the left foot (just after touchdown) in *Nycticebus pygmaeus* walking with a diagonal sequence gait (overhead view); (d) lateral view of (c); (e) swing phase of the left foot (just before touchdown) in *N. pygmaeus* walking with a diagonal sequence gait (overhead view); (f) lateral view of (e). Note that maximum spinal flexion (toward the left foot) occurs during swing phase of the ipsilateral (left) hindlimb in a lateral sequence walking gait (a) and trot (b), but during support phase of the ipsilateral (left) hindlimb in a diagonal sequence walking gait (c, d).

positioning [Figure 9(a), (b)]. In contrast, strepsirhines, like other primates, use a diagonal sequence walking gait (LH–RF–RH–LF) rather than the lateral sequence gait preferred by almost all other tetrapods (Hildebrand, 1967). In a diagonal sequence gait, the contralateral forelimb and hindlimb become widely spaced (i.e., the spine is convex on the contralateral side) when the ipsilateral hindlimb is in support phase and the contralateral forelimb is at or near its touchdown [Figure 9(c), (d)]. Therefore, the occurrence of maximum ipsilateral

flexion during support phase in strepsirhines may serve to facilitate the forward movement and touchdown of the contralateral forelimb. If maximum flexion occurred during ipsilateral swing phase in strepsirhines (as it does in lizards), the spinal convexity produced on the contralateral side would be incompatible with the positioning of the contralateral forelimb and hindlimb (which are closer together than they are during ipsilateral support phase) [Figure 9(e), (f)]. This hypothesized relationship between lateral bending and contralateral forelimb reach in strepsirhines requires further testing, including a more in-depth

analysis of the timing of lateral bending relative to forelimb movements, as well as a consideration of the position of the body axis relative to the substrate and its effects on forelimb reach.

Relationship between velocity and lateral bending

The timing of lateral bending also appears to be influenced by velocity, at least for some of the taxa. For three of the seven subjects included in this part of the analysis (*C. medius* 1, *V. variegata* 2, and *N. pygmaeus*), maximum lateral flexion coincides more closely with touchdown as velocity increases. This pattern suggests that the function of lateral bending during quadrupedalism may be to increase stride length at touchdown, particularly at higher velocities. However, the lack of correlation in the remaining taxa makes it difficult to draw conclusions based on these data alone.

The comparison of velocity effects (in those taxa for which the effects are significant) to those reported for other tetrapods is intriguing. In lizards, maximum lateral flexion coincides more closely with touchdown as velocity *decreases* (Ritter, 1995, 1996), a pattern opposite to that exhibited by these strepsirhines. Based on combined kinematic and electromyographic data, Ritter (1996: 2507) concluded that at low speeds lizards use bending to increase stride length, but at higher speeds “the locomotor function of the trunk may be to provide propulsive force, to provide a stable base for limb support, or aspects of interlimb coordination may become an important determinant of trunk movements”. Based on differences in trunk biomechanics between lizards and mammals (his mammalian data are from the literature) on the one hand, and amphibians on the other, Ritter (1995, 1996) also proposed that amniotes share derived spinal features not found in amphibians. The fact that these strepsirhines do not follow the inferred primitive

amniote pattern suggests that there is diversity in the locomotor function of the trunk in mammals, or more specifically, quadrupedal primates may be distinctive among mammals in this regard (as they are in other biomechanical parameters; see Larson, 1998; Larson *et al.*, 2000).

Finally, there is an interesting contrast between *N. pygmaeus* and *C. medius* 1, but further study is needed to resolve the implications of this contrast due to conflicting data for *C. medius* 2. At higher velocities, lateral flexion becomes less pronounced in *C. medius* 1 but more pronounced in *N. pygmaeus*. By comparison, in lizards (Ritter, 1995, 1996), cats (Carlson *et al.*, 1979) and *Monodelphis* (Pridmore, 1992), lateral bending decreases at higher velocities, but in amphibians, lateral bending increases at higher velocities (Ashley-Ross, 1994a,b). In this respect, *Cheirogaleus* 1 follows the primitive amniote pattern, but *N. pygmaeus* is more amphibian-like. Again, the implications of these results are not clear without further study on larger samples, but the results certainly point to the importance of addressing within-group variability in future research on tetrapod spinal kinematics.

Morphological correlates to lateral bending

It remains to be explained why *Nycticebus* would use more lateral flexion during quadrupedalism than *Loris* (cf. Demes *et al.*, 1990, in which the opposite result is reported using different methods; see above). The difference does not appear to be related to body size, because the values for lateral flexion angle at touchdown and overall range of flexion showed no correlation with body size. Previous research by Demes *et al.* (1990) has shown that *L. tardigradus* has relatively longer limbs (see also McArdle, 1981; Jungers, 1985; Gomez, 1992), a relatively longer stride, and a higher stride frequency when compared to *N. coucang*. *Loris* also has relatively longer limbs than *N. pygmaeus* (Jungers, personal

communication). Perhaps for *Nycticebus*, with its lower stride frequency and relatively shorter limbs, stride length is more dependent on lateral spinal flexion, whereas *Loris* can utilize its relatively longer limbs to increase stride length.

Given the more exaggerated lateral flexion in *Nycticebus* compared to *Loris*, one might also expect a relatively longer lumbar region in the former. Yet the opposite is true—among lorids, lumbar region length is negatively allometric. The smaller taxa, *Loris* and *Arctocebus*, have relatively longer lumbar regions than do the larger *Perodicticus* and *Nycticebus* (*N. coucang*; no data on lumbar region length are available for *N. pygmaeus*) (Demes *et al.*, 1990; Simons, 1998; Simons & Shapiro, 1998). In fact, *Loris* more closely resembles *C. medius* than *Nycticebus* in both lumbar region length (Simons, 1998), and angle of flexion at touchdown. A longer lumbar spine produces more lateral and forward movement of the hip (and thus a greater gain in stride length) for a given angle than does a shorter lumbar spine, which might account for the differences between *Loris* and *Nycticebus* in magnitude of lateral flexion. Alternatively (or in addition), the relatively elongated lumbar regions of *Loris*, *Arctocebus* and *C. medius* compared to the larger lorids (*N. coucang* and *Perodicticus*) might be an adaptation to facilitate cantilevering. Cantilevering is a specialized form of suspensory behavior in which both feet remain on a support while the trunk and forelimbs are stretched toward a second support horizontally (Gebo, 1987; Preuschoft *et al.*, 1995). A long trunk is advantageous for reaching across gaps by cantilevering, but this activity is accompanied by high bending moments (Preuschoft *et al.*, 1995), more easily resisted by (and thus more frequent in) the smaller bodied cheirogaleids and lorids (Oxnard *et al.*, 1990).

The prezygapophyses are more obliquely oriented (relative to a sagittal plane) in lorids than in other strepsirhines (Ankel, 1967;

Curtis, 1995; Shapiro, in prep.) which should permit relatively more lateral flexibility and rotation in the loid lumbar region. According to the kinematic results reported here, *Nycticebus* should have more obliquely oriented prezygapophyses than does *Loris*. This hypothesis is currently being tested (Shapiro, in prep.). It is important to note that variation in prezygapophyseal orientation among lorids may or may not correspond to kinematic variation during quadrupedal walking. That is, all lorids might require obliquely oriented prezygapophyses for facilitating lateral bending or rotation during behaviors such as bridging or climbing, rather than quadrupedal walking. A kinematic study on these behaviors might clarify these issues. Moreover, both taxa might have similar morphological capabilities for bending their spines laterally, but might differ in the behaviors in which the capability is utilized (e.g., see Lauder, 1994).

Conclusions and summary

This study has revealed interspecific variability in the kinematics of the lumbar spine among five genera of strepsirhines. Lateral bending varies among the taxa with respect to magnitude and effects of velocity. With respect to timing of lateral bending (for some of the taxa), maximum lateral flexion occurs closest in time to foot touchdown at faster velocities, suggesting a functional role in increasing hindlimb stride length. On average, maximum lateral flexion occurs just after touchdown, but within support phase. This lateral flexion might be related to forward movement of the contralateral forelimb in conjunction with the distinctive diagonal sequence gait used by all primates. These timing patterns contrast dramatically with those reported for lizards.

Although *Nycticebus* and *Loris* have been described as having a “sinuous or serpentine” gait (Hill, 1953; Walker, 1969,

1974), only *Nycticebus* exhibits significantly more lateral flexion during walking compared to the other taxa. Although this result conflicts to some extent with vertebral morphological patterns of the taxa, it does not preclude the correspondence of morphology with kinematic patterns during behaviors other than walking. Finally, *N. pygmaeus* and *C. medius* 1 (but not *C. medius* 2) differ with respect to the effects of velocity on the magnitude of lateral bending. In *C. medius* 1, lateral flexion decreases as velocity increases, a pattern resembling that reported for other amniotes. By contrast, lateral flexion becomes more pronounced at higher velocities in *N. pygmaeus*, a more amphibian-like pattern. This contrast needs to be re-examined with additional data.

In sum, the kinematic variation reported here suggests that there does not appear to be a "typical" mammalian spinal kinematic pattern, but that lateral bending is influenced by velocity and may be emphasized more by some taxa than by others. This study has also established the importance of considering primate spinal kinematics in the context of that of other tetrapods.

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