

## Tail postures of four quadrupedal leaf monkeys (*Pygathrix nemaeus*, *P. cinerea*, *Trachypithecus delacouri* and *T. hatinhensis*) at the Endangered Primate Rescue Center, Cuc Phuong National Park, Vietnam

Nancy J. Stevens<sup>1</sup>, Kristin A. Wright<sup>2</sup>, Herbert H. Covert<sup>3</sup>, and Tilo Nadler<sup>4</sup>

<sup>1</sup> Ohio University College of Osteopathic Medicine, Department of Biomedical Sciences, 228 Irvine Hall, Athens, OH 45701, USA. <stevensn@ohio.edu> (Corresponding author)

<sup>2</sup> Kansas City University of Medicine and Biosciences, Department of Anatomy, Kansas City, 1750 Independence Avenue, Kansas City, MO 64106-1453. <Kwright@kcumb.edu>

<sup>3</sup> University of Colorado at Boulder, Department of Anthropology, Boulder, CO 80309-0233, USA. <covert@spot.colorado.edu>; <Herbert.Covert@Colorado.edu>

<sup>4</sup> Frankfurt Zoological Society / Endangered Primate Rescue Center, Cuc Phuong National Park, Ninh Binh Province, Vietnam. <t.nadler@mail.hut.edu.vn>

**Key words:** primate locomotion, kinematics, arboreality, limestone langurs, douc monkeys

---

### Summary

The kinematics of colobine locomotion, particularly the folivorous primates of Vietnam, has to date received little attention. Recent work at the Endangered Primate Rescue Center (EPRC) in Cuc Phuong National Park is the first to examine kinematics during arboreal quadrupedal locomotion in these endangered leaf monkeys, revealing marked differences in tail postures among four similarly sized species. During symmetrical walking, doucs (*Pygathrix nemaeus* and *P. cinerea*) typically allow the tail to hang down, falling along the substrate behind them during travel. Delacour's langurs (*Trachypithecus delacouri*) exhibit greater variability, often arching the tail higher in concave-downwards posture. Hatinh langurs (*Trachypithecus hatinhensis*) exhibit the greatest variability in tail posture, often raising the tail in a concave-upwards arc with the tip reaching over the thorax. These patterns are evident in our kinematic data, and may reflect different adaptations to rapid locomotion over varied substrates in the wild. Whereas doucs are typically observed in arboreal settings and utilize forelimb suspensory movements when traveling rapidly, wild Delacour's and Hatinh langurs include steep limestone karst formations to varying extents in their substrate repertoires, and travel rapidly using quadrupedal running and bounding. Further exploration of postural and locomotor adaptations in these taxa is pivotal to their conservation and captive management.

### Hình dáng đuôi của bốn loài khỉ ăn lá (*Pygathrix nemaeus*, *P. cinerea*, *Trachypithecus delacouri*, và *T. hatinhensis*) tại Trung tâm Cứu hộ Linh trưởng Nguy cấp, Vườn Quốc gia Cúc Phương, Việt Nam.

### Tóm tắt

Động học khi di chuyển ở các loài khỉ ăn lá (colobine) còn ít được nghiên cứu, đặc biệt với các loài khỉ ăn lá ở Việt Nam. Ở đây chúng tôi nghiên cứu vấn đề này trên đối tượng là các loài khỉ ăn lá có nguy cơ tuyệt chủng cao được cứu hộ tại Vườn Quốc gia Cúc Phương. Kết quả cho thấy có sự khác biệt rõ rệt về hình dáng đuôi khi di chuyển của bốn loài có kích thước tương đương. Ở các loài

vọc chà vá (*Pygathrix nemaeus* và *P. cinerea*) khi di chuyển bằng bốn chi, đuôi thường thông xuống dưới bề mặt giá đỡ. Còn ở loài vọc mông trắng (*Trachypithecus delacouri*) đuôi thể hiện nhiều hình dáng khác nhau khi di chuyển, đuôi thường nâng cao, uốn cong xuống, mút đuôi chúi xuống. Đối với loài vọc Hà Tĩnh (*Trachypithecus hatinhensis*) đuôi thể hiện đa dạng nhất về hình dáng khi di chuyển, thông thường đuôi nâng cao, uốn cong lên và mút đuôi kéo dài ngang ngực. Các cách biểu hiện trên có liên quan đến động học trong di chuyển của mỗi loài, và chúng có thể phản ánh sự thích nghi của mỗi loài trên các loại giá đỡ khác nhau ngoài tự nhiên. Những quan sát cho thấy ở các loài vọc chà vá thích nghi với đời sống trên cây thường sử dụng kiểu di chuyển treo người bằng hai chi trước để di chuyển nhanh. Trong khi đó các loài vọc thích nghi với đời sống trên núi đá vôi, nơi có sự đa dạng hơn về các loại giá đỡ như vọc mông trắng và vọc Hà Tĩnh lại chạy bằng bốn chi hoặc nhảy. Cần có những nghiên cứu sâu hơn về hình dáng, sự thích nghi khi di chuyển ở các loài trên nhằm phục vụ việc bảo tồn và nuôi dưỡng chúng.

---

## Introduction

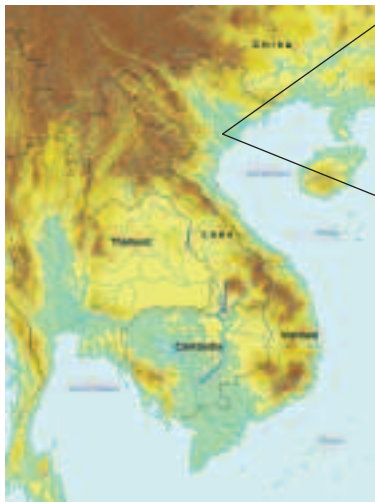
The primates of Vietnam engage in broad range of locomotor behaviors, ranging from the high-velocity ricochet brachiation of the crested gibbons to the deliberate movements of the slow and pygmy lorises. Although the locomotor behaviors of some of these forms are relatively well-understood based on detailed laboratory research (e.g. Demes et al., 1990; Bertram, 2004), notably absent are kinematic studies of colobines, in general, and Vietnam's leaf monkeys in particular. This is likely due to the fact that many of these animals are critically endangered, having remote and restricted ranges in places where collecting locomotor and positional data can present a number of challenges. Moreover, Vietnam's colobines are found in only a handful of captive settings, restricting their availability for laboratory kinematic studies. In an effort to understand variation in kinematics and positional behavior among this fascinating radiation of primates, we have examined differences in tail posture and kinematics during quadrupedal locomotion among captive leaf monkeys housed at the Endangered Primate Rescue Center in Cuc Phuong National Park, Vietnam.

The leaf monkey species included in this study fall within in two distinct groups of Southeast Asian colobines; the odd-nose doucs, represented here by the red-shanked douc (*Pygathrix nemaeus*) and the grey-shanked douc (*P. cinerea*), and the langurs, represented in this study by the Hatinh langur (*Trachypithecus hatinhensis*) and Delacour's langur (*T. delacouri*). All four species are characterized as having long, sweeping tails that exceed the length of their pre-sacral vertebral column (Dao Van Tien, 1985; Nadler, 1997; Nadler et al., 2003). The doucs exhibit a tail that is nearly equal in length to their total head and body length, ending in a tuft of longer hairs. The Hatinh langurs exhibit a similarly formed tail that exceeds total head and body length, and lacks a tuft at the terminal end. Delacour's langurs exhibit an average tail length similar to that found in Hatinh langurs, but are unique among Southeast Asian langurs in possessing a tail that is larger in diameter at its proximal end and more thickly furred (Nadler et al., 2003).

Taking into account the various roles for which different primates employ their tails, and the variation in social behavior, positional repertoire, and tail form across primates, the posture and movements of the tail are of interest (e.g., Garber & Rehg, 1999; Lawler & Stamps, 2002; Schmitt et al., 2005; Larson & Stern, 2006). This structure features in, among other behaviors, alarm calls and displays, it plays an important role in maintaining balance and change of direction during locomotion (Rollinson & Martin, 1981; Dunbar & Badam, 2000; Anapol et al., 2005; Larson and Stern, 2006). Early investigation of the role of the non-prehensile tail in Old World primates determined that longer tails were associated with a higher degree of arboreality, while more

terrestrial species exhibited shorter tails (Rollinson & Martin, 1981). However, subsequent investigations have revealed that the relationships among tail length, substrate use, and positional behavior in primates is more complex than first assumed (Dunbar & Badam, 2000; Anapol et al., 2005; Larson & Stern, 2006). Here, we seek to document whether habitual tail postures and kinematics vary among leaf monkey taxa, and whether there is anything that distinguishes those that prefer the arboreal environment (i.e. *Pygathrix*), from those that incorporate acrobatic locomotion on limestone karst cliffs (i.e. *Trachypithecus*).

Differences in tail and body posture among the leaf monkeys of Vietnam were first observed by Nadler & Ha Thang Long (2000). This contribution complements previous descriptions of the positional behavior of Delacour's langurs (*Trachypithecus delacouri*) and Hatinh langurs (*Trachypithecus hatinhensis*) (Byron & Covert, 2004; Workman & Covert, 2005), and provides the first kinematic examination of tail posture for any of the leaf monkey species considered herein.



**Fig. 1.** Location of study site, Endangered Primate Rescue Center (EPRC) in Cuc Phuong National Park, Vietnam.

### Location

Established in 1962, Cuc Phuong National Park represents the first nationally protected area in Vietnam (Fig. 1). Within the park, the Endangered Primate Rescue

Center (EPRC) represents both an important research facility and a significant conservation site as one of the only rescue and breeding centers for endangered primates in Southeast Asia (Covert et al., 2004). Captive research on the primates of Vietnam provides useful information regarding primate locomotion and positional behavior, as data gathered in controlled settings can be used to develop testable hypotheses concerning behaviors in the wild. The integration of captive and wild data is essential for understanding the ecological tolerances and requirements of these fragile, endangered animals.

### Study sample

As noted previously, the species considered herein include two genera of leaf monkey species ranging in size from 8-12 kg. Hatinh langurs (*Trachypithecus hatinhensis*), Delacour's langurs (*T. delacouri*), red-shanked doucs, and grey-shanked doucs (*Pygathrix nemaeus* and *P. cinerea* respectively). Delacour's langurs are among the most critically endangered primate species in the world, with an estimated total number of less than 300 individuals remaining in the wild. Endemic to limestone mountainous habitats in the Ninh Binh, Ha Nam, Hoa Binh and Thanh Hoa provinces of northern Vietnam, these langurs are restricted to a narrow geographic distribution ranging between 20-21 degrees North and 105-106 degrees East (Nadler et al., 2003). Delacour's langurs are adept arboreal quadrupeds that also engage in locomotion on steep karst cliff faces, exhibiting dramatic, sweeping motions of their long tails, along with a broad range of locomotor behaviors as they negotiate these challenging near-vertical substrates (Fig. 2).



**Fig. 2.** Delacour's langurs in Van Long Nature Reserve. Photo: T. Nadler.

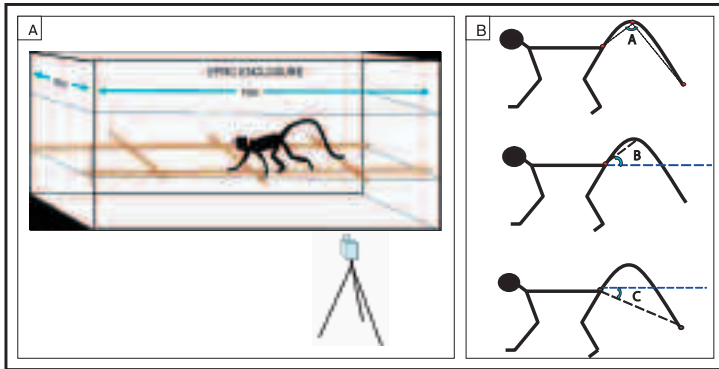
recent times (Nadler et al., 2003). A close relative of the Laotian langur (*Trachypithecus laotum*), there are thought to be less than 700 Hatinh langurs alive today, with hunting and habitat loss continuing to exert pressure on the remaining populations. Little is known of their habits in the wild, although they also reportedly use caves as sleeping sites, and at least at the EPRC, they appear to be more active than *T. delacouri* (T. Nadler, pers. obs.).

Grey-shanked doucs are slightly larger than the Hatinh and Delacour's langurs, while the red-shanked doucs are similarly sized (Nadler et al., 2003). Both douc species appear to move more slowly than either the Hatinh or Delacour's langurs. In addition to hunting pressure, doucs are susceptible to habitat loss, with many populations isolated in small and unprotected forest fragments. Red-shanked doucs inhabit forested areas with some limestone karsts in north-central Vietnam, whereas grey-shanked doucs are primarily found in central Vietnam, although *P. nemaeus* and *P. cinerea* are thought to exist in sympatry in some areas along the boundaries of the species' ranges (Nadler et al., 2003). A third species, the black-shanked douc (*P. nigripes*) is not well represented in captivity at the EPRC and hence not considered in this study. Notably, none of the *Pygathrix* species have been reported to use limestone karst cliffs with high frequency during locomotion, however the black-shanked douc has been reported to use granite outcroppings found within its habitat relatively often (Ha Thang Long & Nadler, 2007). Interestingly the tail length of black-shanked doucs exceeds that of red- and grey-shanked doucs by about 100mm on average, hence this taxon may provide an interesting perspective on tail posture in a future study. Along with Hatinh langurs, red- and black-shanked doucs are listed as Endangered in the IUCN Red List of Threatened Species (Southeast Asian Mammal Databank, 2006). Moreover, Delacour's langurs and grey-shanked doucs are among the world's 25 most critically endangered primate species (Mittermeier et al., 2007). The need for more information on the habits and ecological constraints of these animals sets a context for a detailed examination of their locomotor biology.

## Methods

### Kinematic data collection

Several adult male and female Hatinh (n=7), Delacour's (n=5) langurs, red-shanked (n=6), and grey-shanked (n=4) doucs were filmed in the EPRC, Cuc Phuong National Park, Vietnam between July, 2005 and May, 2006. Housed in semi-naturalistic enclosures, subjects were filmed walking along horizontal supports approximately 5cm in diameter. Following methods described in Stevens



**Fig. 3.** A) Kinematic data collection setup using semi-naturalistic enclosures at the Endangered Primate Rescue Center. B) Angles measured in this study.

(2003) and Stevens et al. (2006), cameras were positioned in lateral view at a distance of greater than 5m to reduce effects of parallax (Fig. 3A). Frame rates were optimized to catch rapid movements by splitting 30Hz fields to achieve 60Hz, and shutter speeds were set to reduce motion blur. For each species, 15 strides without visible changes in speed or direction were analyzed. Video clips were imported into Peak Motus and kinematic points along the back, limbs and tail were digitized at forelimb and hind limb touchdown, midsupport and lift off events. Differences in tail posture were quantified using three different measures (Fig. 3B): Tail inflection angle (Angle A) is defined by three kinematic points: the base of the tail, the inflection point of the greatest tail curvature, and the tip of the tail. This angle describes the relative convexity/concavity of the tail posture in lateral view. Angle B is defined by the tail's inflection point, the base of the tail, and an imaginary x-axis (horizontal line) drawn through the tail base marker. This angle describes the relative projection of the midpoint of the tail above or below the tail base. The final angle, Angle C, is defined by the tail tip, the tail base, and an imaginary x-axis through the tail base marker. Angle C describes the degree to which the tail tip projects above or below the tail base.

### Kinematic statistical analyses

Because kinematic data can not be expected to follow a normal distribution, data were rank-transformed prior to analysis of variance. Rank transformation permits analysis of variance without loss of power in datasets that are not normally distributed (Conover & Iman, 1981). Kinematic differences correlated with velocity may simply reflect differences in locomotor speed, hence speed-correlated variables were also examined using analysis of covariance with locomotor velocity as the covariate.

### Behavioral data collection

Kinematic analyses were supplemented with behavioral data on posture and locomotor mode. Instantaneous focal animal sampling (Altmann, 1974) and bout sampling were used simultaneously to record positional behavior and posture on the substrate (Table 1). Instantaneous samples were recorded at 25 second intervals for several hours on male and female adult Hatinh langurs (n=3), Delacour's langurs (n=3), grey-shanked doucs (n=2) and red-shanked doucs (n=3), yielding over 4500 observations in all. One benefit of observing these species at the EPRC is that the enclosures are relatively uniform in size and construction, making it possible to rule out variation in structural environment as a possible causative factor when interpreting similarities or differences in behavioral patterns between the four leaf monkey species. Nonetheless, due to low numbers of individuals and observations, data reported herein are preliminary in nature and are interpreted with caution.

Several tail postures were identified that could be quickly assessed and recorded by the behavioral observer. This lends ecological relevance to the study of kinematic “hows” by providing frequency data on “how often” a given tail posture was assumed. Tail postures were sorted into five major categories: tail hanging down (Fig. 4A), tail on branch (Fig. 4B), tail back (Fig. 4C), tail back with a concave-upwards arch (Fig. 4D), tail back with a concave-downwards arch (Fig. 4E). Tail posture frequencies in each category were compared across species and in relation to locomotor mode.

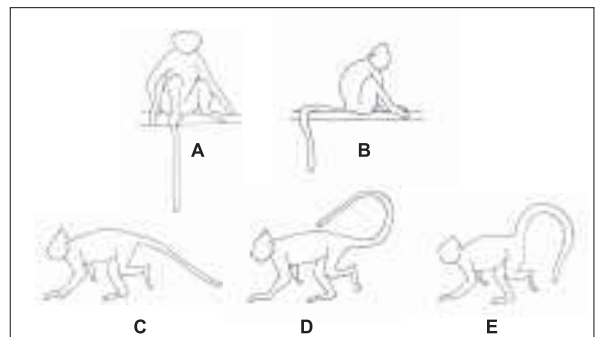
**Results and Discussion**

**Tail kinematics**

Because the leaf monkey species included in this study do not differ greatly in body size or available habitat type, our null hypothesis was that they would not exhibit significant differences in tail posture or locomotor/ positional behavior. Interestingly, kinematic analysis revealed that tail postures differ considerably among species. In all taxa, the tail inflection angle (Angle A) remained relatively constant throughout the stride cycle (Fig. 5A). Both douc species, along with the Delacour’s langurs, exhibited a concave downward arch of the tail as reflected by positive tail inflection angles (Fig. 5A), whereas Hatinh langurs exhibited a concave-upward tail inflection (Fig. 5A). Tails were significantly more arched in Hatinh langurs at all kinematic events. For all of the leaf monkeys, a strong correlation was observed between tail inflection and speed ( $p < .005$  for all species at all kinematic events; Table 2), with tails drooping and trailing along the support at lower speeds and rising into a higher arch at more rapid speeds. Doucs

**Table 1.** Ethograms of postures and locomotor modes recorded in this study.

Postures	
QS	Quadrupedal stand
SP	Sit perpen di cular to substrate
SPL	Sit parallel to substrate
PV	Prone ventral
PD	Prone dorsal
BP	Bipedal stand
S	Suspension (any suspensory posture)
SG	Sit on ground
Motions	
QW	Quadrupedal walk
QF	Fast quadrupedalism
QB	Quadrupedal bound
LU	Leap up (can be hands or feet first)
LD	Leap down (can be feet or feet first)
CU	Climb up
CD	Climb down (can be hands or head first)
AS	Arm swing (any suspensory motion)
BPW	Bipedal walk
PU	Pull up (can be one handed or two handed)
DROP	Drop down from substrate

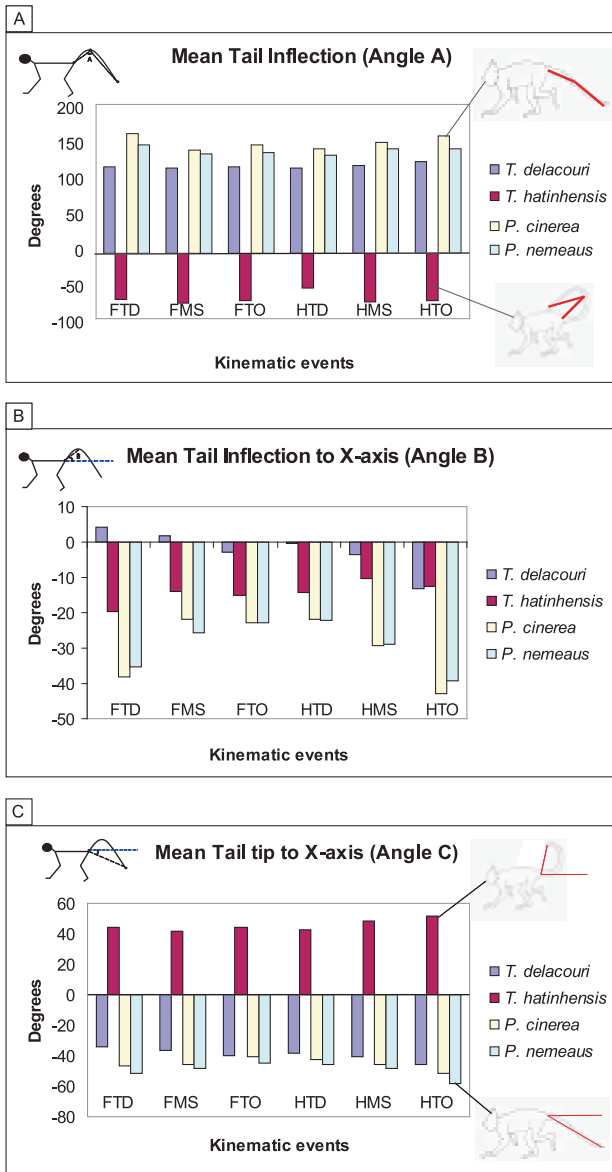


**Fig. 4.** Tail postures recorded in this study. A. Tail Hang Down (THD/TD) B. Tail On Branch (TOB/DB) C. Tail Back (TO/TB) D. Tail Back Concave Up (TA) E. Tail Back Concave Down (TQ)

**Fig. 4.** Tail postures recorded in this study.

**Table 2.** Significance levels for comparisons among langur species in this study.

	person	speaman	anova	ancova
Fore TD	0.000	0.000	0.000	0.001
Fore MS	0.010	0.010	0.000	0.001
Fore TO	0.000	0.000	0.000	0.000
Hlnd TD	0.001	0.001	0.000	0.005
Hlnd MS	0.000	0.000	0.000	0.000
Hlnd TO	0.000	0.000	0.000	0.000



**Fig. 5.** Tail kinematics and forelimb and hind limb events. FTD=forelimb touch down; FMS=forelimb midsupport; FTO=forelimb lift off; HTD=hind limb touch down; HMS=hind limb midsupport; HTO=hind limb lift off. N=15 for each species. A) Mean tail inflection angle (Angle A) at forelimb and hind limb events. Note concave upward posture in *T. hatinhensis*—comparisons between all other species and *T. hatinhensis* exceed significance levels of  $p < 0.05$ . B) Mean mid-tail angle (Angle B), made by inflection point, the base of tail and an imaginary horizontal line through the base of the tail. Tails are typically less arched in *Pygathrix* than in *Trachypithecus*. C) Mean tail tip angle (Angle C), defined as the angle between the tip of the tail, the base of the tail, and an imaginary horizontal line through the tail base. Note that tail tip generally is carried above the level of the substrate in *T. hatinhensis*, in contrast with below-substrate tail tip typically exhibited by the other species in the study.

never attained the locomotor velocities of the *Trachypithecus* species, but even so, at higher speeds their tails exhibited a slight inferiorly-concave arch. The highest speeds were observed in *T. delacouri* ( $p < .01$  for all events), which may have contributed to their more acute mean tail inflection angle relative to doucs.

Further analyses revealed that Delacour's langurs tend to carry the body of the tail slightly higher than do Hatinh langurs or doucs, as revealed by higher values for Angle B (Fig. 5B). Interestingly, the tail inflection to x-axis angle (Angle B) suggests more change in tail position during the stride cycle than did the tail inflection angle, yet no correlation was observed between Angle B and travel velocity. Perhaps not surprisingly, the tail tip to x-axis angle (Angle C) was a good discriminator of the Hatinh langurs as they tend to arch their tails concave-upwards, particularly at higher speeds, such that the tail tip is in a much different position than is observed in the Delacour's langurs and the doucs (Fig. 5C). As Hatinh langurs exploit similar habitat types as the other leaf monkeys, there is not a clear explanation for their unique tail posture at this time, but we are pursuing more detailed studies of axial postcranial morphology and will soon have the opportunity observe this species in its natural habitat.

**Positional behavior**

Patterns in tail kinematics may reflect differences in postural and locomotor preferences between the leaf monkey species. For example, Delacour's langurs prefer to sit the majority of the

time, whereas Hatinh langurs tend to use prone positions and spend more time on the ground. Moreover, Hatinh langurs exhibit higher frequencies of quadrupedal walking than do Delacour's langurs (Fig. 6), whereas the latter leap and bound more frequently ( $p < 0.1$ ). In contrast, doucs spend a significant portion of time in forelimb suspensory postures (48-60%) and less time walking and leaping than do either of the *Trachypithecus* species.

With respect to tail posture, the most notable difference among the four species is that Delacour's and Hatinh langurs exhibit a great deal more variability in tail postures than do the doucs, frequently using tail postures that involve holding the tail up and/or arched over the body (TA), or back away from the body (TQ) (Fig. 7A-B). Only Delacour's langurs used the TQ tail position, whereas only Hatinh

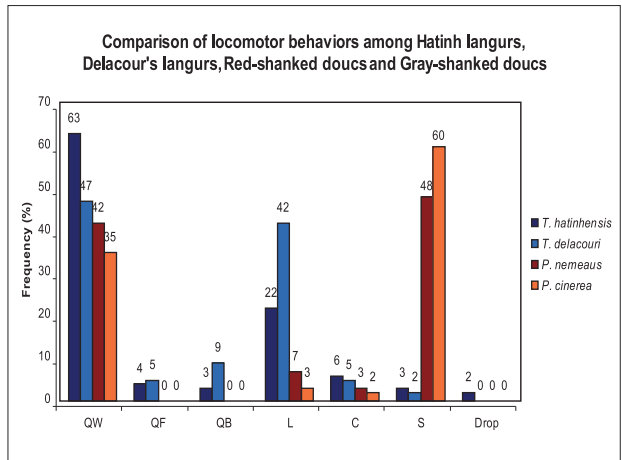


Fig. 6. and postural behavior by category in the four leaf monkeys.

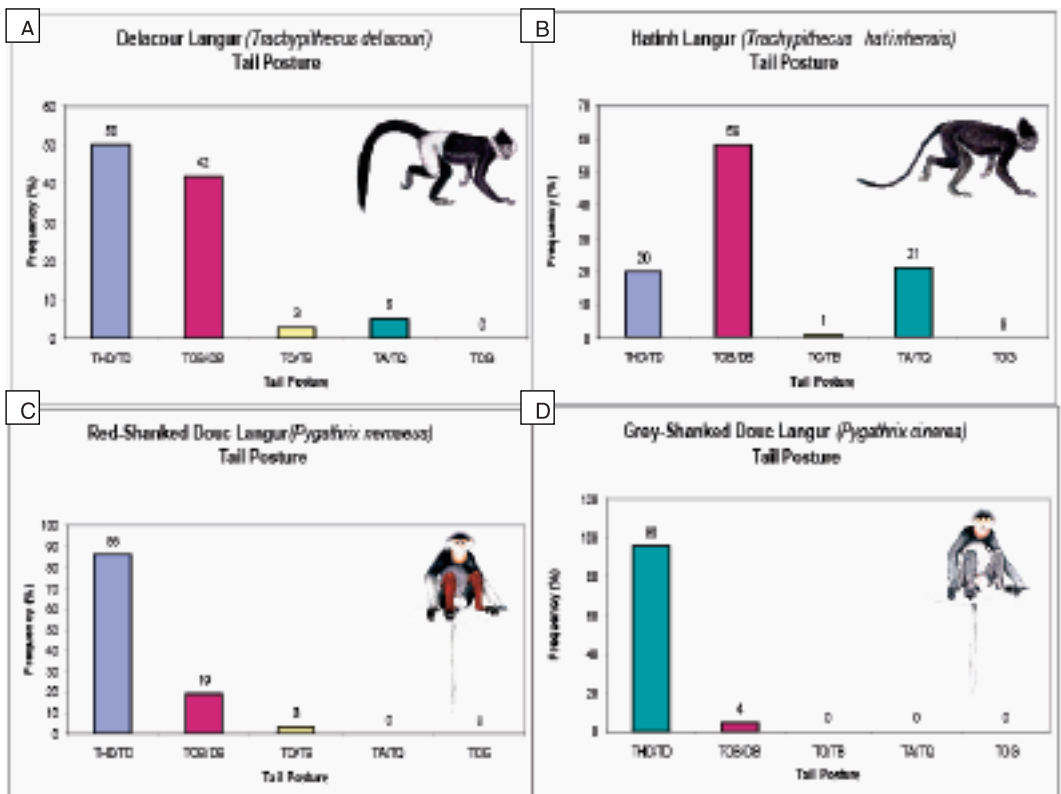
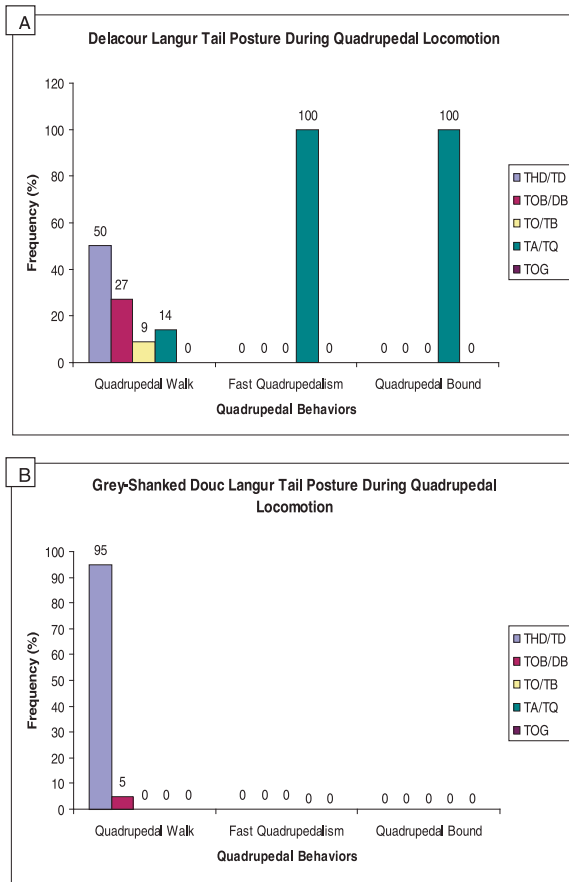


Fig. 7. Percent time spent exhibiting different tail postures by the four leaf monkeys. A) *Trachypithecus delacourii*, B) *T. hatinhensis*, C) *Pygathrix nemeaus*, and D) *P. cinerea*.





**Fig. 8.** Tail posture during quadrupedal locomotion in A) *Trachypithecus delacouri*, and B) *Pygathrix cinerea*. Note that whereas the Delacour's langur engages in fast quadrupedal walking and bounding in addition to slow walking, quadrupedal locomotion in grey-shanked doucs is typically slow. Patterns are similar in each of their congeners.

respectively) (e.g. Fig. 8B). Interestingly, neither the red-shanked nor the grey-shanked doucs were observed using faster modes of quadrupedalism or bounding. This may relate to the use of more suspensory modes for faster travel in *Pygathrix* species.

## Discussion and conclusions

Recent work in Cuc Phuong National Park is the first to document detailed locomotor kinematics among the colobines of Vietnam. This study reveals marked differences in tail postures among four leaf monkey species explored herein. During symmetrical walking, doucs (*Pygathrix nemaeus* and *P. cinerea*) typically allow the tail to hang down, falling along the substrate behind them during travel. Delacour's langurs (*Trachypithecus delacouri*) exhibit greater variability, frequently arching the tail higher in concave-downwards posture. Hatinh langurs (*Trachypithecus hatinhensis*) exhibit the most variability in tail carriage, often raising the tail into a concave-upwards arc with the tip reaching over the thorax. These patterns may reflect phylogeny and/or different locomotor adaptations used in the wild. Genetic findings detail a deep split in the "limestone langurs" (e.g.

langurs were observed using the TA tail posture. The most frequent tail postures for both *Trachypithecus* species allowed the tail to hang freely in a pendulous position (THD/TD), or draped over a substrate (TOB/DB) (Fig. 7A-B). Delacour's langurs used the TQ tail position 100% of the time when they were walking fast, or bounding (Fig. 8A).

During slower quadrupedalism they tended to let the tail hang down (50%) or rest on a substrate (27%). TQ tail position was used only 14% of the time during walking. Hatinh langurs used the TA tail position almost exclusively during quadrupedal locomotion (87% for walk, 100% for fast quadrupedalism, and 100% for bounding). This suggests that tail posture may vary as a function of locomotor mode and/or velocity. The only tail postures observed for the red-shanked and grey-shanked doucs were postures that allowed the tail to hang freely in a pendulous position (THD/TD), drape on substrate (TOB/DB), or that held the tail up off of the substrate, but straight out in back of the body (TO/TB) (Fig. 7C-D). Both the red-shanked and grey shanked doucs used THD/TD most frequently during quadrupedal walking (84% and 95%,

Roos et al., 2001) with a northern group including *T. delacouri*, *T. francoisi*, *T. poliocephalus*, and *T. leucocephalus*, and a southern group including *T. hatinhensis*, *T. laotum*, and in some analyses *T. ebenus*. Anecdotally, tail posture with each of these genetic/geographic groups of *Trachypithecus* is very similar, with the northern species exhibiting concave-downward tail carriage and the southern species exhibiting concave-upward postures.

From the standpoint of differing locomotor adaptations, doucs differ from *Trachypithecus* species in exhibiting relatively little overall movement of the tail during quadrupedal locomotion. These species typically use quadrupedal behaviors to move slowly, transitioning to suspensory locomotion to travel at higher speeds. In contrast, Delacour's and Hatinh langurs exhibit a range of locomotor speeds during quadrupedalism, favoring fast quadrupedalism and bounding over arm-swinging behaviors (Wright et al., in press) and may incorporate sweeping motions of their tails to assist with balance when negotiating steep limestone karst formations in the wild. Further exploration of habitat use and locomotor adaptation of leaf monkeys is needed to test these ideas, and better knowledge of their natural habitats is pivotal for conservation and captive management of these critically endangered forms.

## Acknowledgments

We thank Mr. Truong Quang Bich, Director of Cuc Phuong National Park, and Mr. Do Van Lap, Chief of Scientific and International Collaboration Department for permission to work at the Endangered Primate Rescue Center (EPRC). Partial funding was provided by the Zoological Society of San Diego, and the College of Osteopathic Medicine at Ohio University. Special thanks also go to Patrick O'Connor, Barth Wright, Sherri Steele, Larry Ulibarri, Jonathan O'Brian, Lea Ann Jolley, Nguyen Thi Thu Hien, Le Khac Quyet, Ulrike Streicher, Elke Schwierz, and all of the staff at the EPRC for their support, advice, and friendship.

## References

- Altman J** (1974): Observational study of behavior: Sampling methods. *Behaviour* 49, 227-265.
- Anapol F, Turner TR, Mott CS & Jolly CJ** (2005): Comparative postcranial body shape and locomotion in *Chlorocebus aethiops* and *Cercopithecus mitis*. *Am. J. Phys. Anthropol.* 127, 231-239.
- Bertram JE** (2004): New perspectives on brachiation mechanics. *Am. J. Phys. Anthropol.* 125(S39), 100-117.
- Byron C & Covert HH** (2004): Unexpected locomotor behavior: brachiation by an Old World monkey from Vietnam. *J. Zool. Lond.* 263, 101-106.
- Huang C & Y Li** (2005): How does the white-headed langur (*Trachypithecus leucocephalus*) adapt locomotor behavior to its unique limestone hill habitat? *Primates* 46, 261-267.
- Conover WJ & Iman RI** (1981): Rank transformations as a bridge between parametric and nonparametric statistics. *Am. Stat.* 35, 124-133.
- Covert HH, Workman C & Byron C** (2004): The EPRC as an important research center: Ontogeny of locomotor differences among Vietnamese colobines. In: Nadler, Streicher & Ha Thang Long (eds.): *Conservation of Primates in Vietnam*; pp. 121-129. Frankfurt Zoological Society, Hanoi.
- Dagosto M & Gebo D** (1998): Methodological issues in studying positional behavior. In: Strasser, Fleagle, Rosenberger & McHenry (eds.): *Primate Locomotion: Recent Advances*; pp. 5-29. New York, Plenum Press.
- Dao Van Tien** (1985): Khảo Sát Thú, Ở Miền Bắc Việt Nam, Nhà Xuất Bản Khoa Học Và Kỹ Thuật, Hanoi.
- Demes B, Jungers WL & Nieschalk U** (1990): Size and speed related aspects of quadrupedal walking in slender and slow lorises. In: Jouffroy, Stack & Niemetz (eds): *Gravity, Posture and Locomotion in Primates*; pp. 175-198. Florence, Il Sedicesimo.
- Dunbar DC & Badam GL** (2000): Locomotion and posture during terminal branch feeding. *Int. J. Primat.* 21, 649-669.
- Fleagle JG** (1977a): Locomotor behavior and skeletal anatomy of sympatric Malaysian leaf-monkeys (*Presbytis obscura* and *Presbytis melalophos*). *Yrbk. Phys. Anthropol.* 20, 440-453.

- Fleagle JG** (1977b): Locomotor behavior and muscular anatomy of sympatric Malaysian leaf-monkeys (*Presbytis obscura* and *Presbytis melalophos*). Yrbk. Phys. Anthrop. 46, 297-308.
- Fleagle JG** (1979): Primate positional behavior and anatomy: naturalistic and experimental approaches. In: Morebeck, Preuschoft & Gomberg (eds.): Environment Behavior and Morphology: Dynamic interactions in Primates; pp. 313-325. Gustav Fischer, New York.
- Fleagle JG** (1980a): Locomotion and posture. In: Chivers (ed.): Malayan Forest Primates; pp. 1-19. New York, Plenum.
- Fleagle JG** (1980b): Size and adaptation in primates. In: Jungers (ed.): Size and scaling in primate biology; pp. 1-19. Plenum, New York.
- Fleagle JG** (1988): Primate Adaptation and Evolution. Academic Press, New York.
- Fleagle JG & Mittermeier RA** (1980): Locomotor behavior, body size and comparative ecology of seven Surinam monkeys. Am. J. Phys. Anthrop. 52, 301-314.
- Fleagle JG & Meldrum DJ** (1988): Locomotor behavior and skeletal morphology of two sympatric pitheciine monkeys, *Pithecia pithecia* and *Chiropotes satanas*. Am. J. Primatol. 16, 227-249.
- Garber PA & Rehg JA** (1999): The ecological role of the prehensile tail in White-faced Capuchins (*Cebus capuchinus*). Amer. J. Phys. Anthrop. 110, 325-339.
- Groves C** (2004): The what, why and how of primate taxonomy. Int. J. Primat. 25, 1105-1126.
- Ha Thang Long & Nadler** (2007): Rapid assessment on the status of black-shanked doucs (*Pygathrix nigripes*) on Hon Heo Peninsula, Khanh Hoa Province. Report to Frankfurt Zoological Society.
- Jones T & Ehardt CL** (2005): The highland mangabey *Lophocebus kipunji*: a new species of African monkey. Science 308, 1161-4.
- Larson SG & Stern JT** (2006): Maintenance of above-branch balance during primate arboreal quadrupedalism: Coordinated use of forearm rotators and tail motion. Am. J. Phys. Anthrop. 129, 71-81.
- Lawler RR & Stamps C** (2002): The relationship between tail use and positional behavior in *Alouatta palliata*. Primates. 43, 147-152.
- Mittermeier RA, Ratsimbazafy J, Rylands AB, Williamson L, Oates JF, Mbora D, Ganzhorn JU, Rodriguez-Luna E, Palacios E, Heymann EW, Cecilia M, Kierulff, Yongcheng L, Supriatna J, Roos C, Walker S & Aguiar JM** (2007): Primates in Peril: The world's 25 most endangered primates, 2006-2008. Primate Conservation 22, 1-40.
- Morbeck ME** (1977): Positional behavior, selective use of habitat substrate and associated non-positional behavior in free ranging *Colobus guerza* (Ruppel, 1835). Primates 18, 35-58.
- Nadler T** (1997): A new subspecies of Douc langur, *Pygathrix nemaues cinereus* ssp. nov. Zool. Garten (NF) 67(4), 165-176.
- Nadler T** (2004): Distribution and status of the Delacour's langur (*Trachypithecus delacouri*) and recommendations for its long-term conservation. In: Nadler, Streicher, Ha Thang Long (eds.): Conservation of Primates in Vietnam; pp. 63-71. Frankfurt Zoological Society, Hanoi.
- Nadler T & Baker LR** (2000): Release of a group of Hatinh langurs (*Trachypithecus laotum hatinhensis*) into a semi-wild facility to associate with gibbons at the EPRC, Vietnam. Endangered Primate Rescue Center Newsletter 5, 18-20.
- Nadler T & Ha Thang Long** (2000): The Cat Ba Langur: Past, Present and Future – The Definitive Report on *Trachypithecus poliocephalus*, the World's Rarest Primate. Frankfurt Zoological Society, Hanoi.
- Nadler T, Momberg F, Nguyen Xuan Dang & Lormee N** (2003): Leaf Monkeys: Vietnam Primate Conservation Status Review 2002 – Part 2. Fauna & Flora International-Vietnam Program and Frankfurt Zoological Society, Hanoi.
- Nadler T & Streicher U** (2004): The Primates of Vietnam - an overview. In: Nadler, Streicher & Ha Thang Long (eds.): Conservation of Primates in Vietnam; pp. 8-13. Frankfurt Zoological Society, Hanoi.
- Napier JR & Napier PH** (1967): A Handbook of Living Primates. Academic Press, London.
- Nguyen Ba Thu** (2004): Conservation of Primates in Vietnam. In: Nadler, Streicher & Ha Thang Long (eds.): Conservation of Primates in Vietnam; pp. 3-4. Frankfurt Zoological Society, Hanoi.
- Ripley S** (1967): The leaping of langurs a problem in the study of locomotor adaptation. Am. J. Phys. Anthrop. 26, 149-170.
- Ripley S** (1977): Grey zones and grey langurs: is the "semi" concept seminal? Yrbk. Phys. Anthrop. 20, 376-394.
- Rollinson J & Martin RD** (1981): Comparative aspects of primate locomotion with special reference to arboreal cercopithecines. Symp. Zool. Soc. Lond. 48, 377-427.
- Roos C, Nadler T, Zhang YP & Zischler H** (2001): Molecular evolution and distribution of the superspecies *Trachypithecus [francoisi]*. Folia Primatol. 72, 181-182.
- Rowe N** (1996): The Pictorial Guide to the Living Primates. Pogonius Press, East Hampton.
- Schmitt D, Rose MD, Turnquist JE & Lemelin P** (2005): Role of the prehensile tail during ateline locomotion: experimental and osteological evidence. Am. J. Phys. Anthropol. 126, 435-446.

- Shapiro L** (1993): Functional morphology of the vertebral column in primates. In: Gebo (ed.): Postcranial Adaptation in Nonhuman Primates; pp. 121-149. DeKalb, Northern Illinois University Press.
- Sokal R & Rohlf F** (1981): Biometry (3rd edition). WH Freeman, San Francisco.
- Southeast Asian Mammal Databank** (2006): <http://www.ieaitaly.org/samd>.
- Spencer M & Spencer G** (1995): Technical note: Video-based three dimensional morphometrics. *Am. J. Phys. Anthropol.* 96, 443-453.
- Stevens NJ** (2003): The influence of substrate size, orientation and compliance upon prosimian arboreal quadrupedalism. PhD Dissertation, p 534. Stony Brook University, New York.
- Stevens NJ, Schmitt DO, Cole TM & Chan L-K** (2006): Technical note: Out of plane angular correction based on a trigonometric function for use in two-dimensional kinematic studies. *Am. J. Phys. Anthropol.* 129, 399-402.
- Workman C & Covert HH** (2005): Learning the ropes: the ontogeny of locomotion in red-shanked douc (*Pygathrix nemaeus*), Delacour's (*Trachypithecus delacouri*), and Hatinh langurs (*Trachypithecus laotum hatinhensis*). *Positional Behavior. Amer. J. Phys. Anthropol.* 128, 371-380