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Comparisons of Suspensory Behaviors Among *Pygathrix cinerea*, *P. nemaeus*, and *Nomascus leucogenys* in Cuc Phuong National Park, Vietnam

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Abstract In our study at the Endangered Primate Rescue Center of Cuc Phuong National Park, Vietnam, we aimed first to assemble a positional behavioral profile of captive gray-shanked (*Pygathrix cinerea*) and red-shanked (*P. nemaeus*) doucs that relates to the use of forelimb suspensory postures and arm-swinging locomotion. The profile is of interest because researchers have documented that red-shanked doucs more frequently use suspensory postures and locomotions than other colobines do. We confirmed that red-shanked doucs commonly use suspensory positional behaviors and also that gray-shanked doucs use suspensory behaviors at similar or even higher frequencies than those of red-shanked doucs. Our second goal was to assemble a preliminary kinematic profile of suspensory locomotion in *Pygathrix* within the context of the arm-swinging locomotion exhibited by northern white-cheeked gibbons, *Nomascus leucogenys*. Mean forelimb angles at initial contact and release of arm-swinging behaviors were remarkably consistent among gibbons and doucs despite the fact that gibbons typically used more continuous brachiation. Doucs also exhibit a greater range of forelimb angles than gibbons do. In addition, trunk orientation tends to be less vertical at initial contact for doucs than for gibbons, perhaps owing to the frequent use of quadrupedal sequences directly before or after

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forelimb suspension. Our behavioral and kinematic analyses add to the emerging realization that *Pygathrix* is capable of, and frequently expresses, a range of suspensory positional behaviors, including brachiation.

Keywords forelimb suspension · positional behavior · *Pygathrix cinerea* · *Pygathrix nemaeus*

Introduction

Primatologists have long been interested in the diverse range of locomotor behaviors exhibited by modern primates. By the mid-1960s, scholars had developed a classification system to describe locomotor behaviors of both extant and extinct primates (Prost 1965). They described primates as arboreal and terrestrial quadrupeds, vertical clingers and leapers, knuckle-walkers, and slow climbers (Ashton and Oxnard 1964; Napier and Napier 1967). Discerning the frequencies of different locomotor behaviors in relation to substrate availability became the objective of studies of positional behavior in the natural setting (Morbeck 1977; Ripley 1977) and formed the foundation for studies examining kinematic and kinetic details in the captive realm. Against this backdrop, researchers have observed forelimb suspensory postures and locomotion in extant primate clades.

Historically, researchers have used the term brachiation to describe a variety of arm-swinging behaviors. Typically, they termed the continuous bimanual or ricochetal progression characteristic of lesser apes true brachiation in both the natural and laboratory settings (Fleagle 1974; Preuschoft and Demes 1984; Swartz 1989; Tuttle 1968) and the more variable bimanual behaviors of African apes and orangutans modified brachiation (Andrews and Groves 1976; Napier and Napier 1967). Napier and Davis (1959) introduced the term semibrachiation to account for forelimb suspension in a diverse array of monkeys in Africa, Asia, and South America. Primatologists did not universally adopt such language, in light of the paucity of naturalistic information available for many semibrachiators and the ambiguity of the prefix semi- to describe any locomotor or postural behavior (Ripley 1977).

Studies of positional behavior in platyrrhines revealed that both *Ateles* and *Lagothrix* frequently employed suspensory behaviors, but also found that their use of prehensile tails during arm-swinging locomotion was associated with important kinematic differences, i.e., a less orthograde trunk posture than that exhibited by gibbons and siamang (Cant 1986; Cant *et al*. 1997, 2003; Erickson 1963; Fleagle 1976; Fleagle and Mittermeier 1980; Mittermeier 1978; Mittermeier and Fleagle 1976). Meanwhile, field studies of positional behavior in African and Asian colobines demonstrated that arboreal quadrupedalism and leaping constituted their predominant forms of locomotion, whereas suspensory postures and movement patterns were relatively rare (Fleagle 1977a, b, 1978; Mittermeier and Fleagle 1976; Morbeck 1977; Ripley 1967, 1979; Rose 1978). Such observations concurred with captive work by Avis (1962), who argued that Old World monkeys did not routinely perform the suspensory movements that characterize the locomotor profile of greater and lesser apes. Interestingly, the single outlier in the Avis study was *Trachypithecus obscurus* (dusky leaf monkey: Brandon-Jones *et al*. 2004; Groves 2001). Though primarily quadrupedal in the experimental cages, all 5 individuals routinely engaged in bimanual locomotion using the bars at the top of their cages, causing Avis (1962) to comment that their arm-swinging behavior was virtually the same as that of the apes in her study: chimpanzees (*Pan*), orangutans (*Pongo*), and gibbons (*Hylobates*).

After the work of Avis (1962), Fleagle (1976, 1977a, b, 1978), and Ripley (1967, 1977) researchers have published relatively little on the posture and locomotion of any Asian colobine. Recent studies of the natural behavior of endangered Southeast Asian leaf monkeys are beginning to yield important new data on little-known species such as the doucs (*Pygathrix* spp.) and their close relatives, the snub-nosed monkeys (*Rhinopithecus* spp.; Bleisch *et al*. 1993; Byron and Covert 2003, 2004; Byron *et al*. 2002; Covert and Byron 2002; Covert *et al*. 2006a, b; Jablonski 1998; Kirkpatrick 1998, 2007; Lippold 1995, 1998; Nadler *et al*. 2003, 2004; Pham Nhat 1994; Workman and Covert 2005; B. Wright *et al*. 2008). Research on captive red-shanked doucs revealed unexpectedly high frequencies of bimanual locomotion and forelimb suspensory postures (Byron and Covert 2003, 2004; Workman and Covert 2005). Via a multidisciplinary and integrated approach to explore primate functional morphology and behavior (Morbeck *et al*. 1979), we combined naturalistic methods for the collection of positional behavior with field-based kinematics to examine suspensory behavior in doucs.

We studied doucs at the Endangered Primate Rescue Center (EPRC) of Cuc Phuong National Park, Vietnam, with 2 primary goals. The first was to assemble a positional behavioral profile of captive gray-shanked (*Pygathrix cinerea*) and red-shanked (*P. nemaeus*) doucs that relates to the use of forelimb suspensory postures and arm-swinging locomotion, allowing us to address the question: How often do *Pygathrix* spp. engage in suspensory behaviors? The second goal was to assemble a preliminary kinematic profile of suspensory locomotion in *Pygathrix* within the context of the arm-swinging locomotion exhibited by northern white-cheeked gibbons, *Nomascus leucogenys*. This enabled us to examine whether doucs engage in forelimb and trunk postures similar to those of gibbons during arm-swinging, and to describe how *Pygathrix* spp. perform suspensory locomotion.

Methods

Study Site

Following procedures reviewed and approved by both the Kansas City University of Medicine and Biosciences and the Ohio University Institutional Animal Care and Use Committees (IACUC), we collected behavioral and kinematic observations from captive doucs and gibbons at the EPRC in Cuc Phuong National Park, within the Nho Quan District of Ninh Binh Province, Vietnam, *ca.* 120 km south of Hanoi. The EPRC is internationally recognized as one of the world's premiere centers for the conservation of Southeast Asian primates, supporting >140 individuals that represent 15 Indochinese primate taxa. It is the only institution in the world to house many of Vietnam's primate species, several of which are endangered or critically endangered (Covert *et al*. 2004; Mittermeier *et al*. 2007; Nadler *et al*. 2003, 2004). We obtained permission to conduct the research from the appropriate national authorities in

Vietnam and the director of Cuc Phuong National Park, and performed the studies under the supervision of the director of the EPRC.

The enclosures at the EPRC afford an unparalleled opportunity to study a diverse radiation of primates that are not only difficult to observe in the wild owing to their conservation status, but are also historically relatively understudied, particularly from the standpoint of positional behavior (Byron and Covert 2004). Our focal subjects are housed in nearly identical chain-link 10×5.5×3.5 m outdoor enclosures. Each enclosure contains a similar variety of substrates, including bamboo poles ranging in diameter from <2 cm to >8 cm, natural tree branches of similar size, ropes, and 1×1.5-m wooden platforms. The similarities permit a degree of experimental control across comparisons of multiple primate species. Conditions at the EPRC allow us to bring together behavioral observations and experimental kinematic protocols to engage in a synthetic approach aimed at quantifying and describing a broad range of locomotor and postural behaviors.

Behavioral Data Collection and Analyses

We observed adult male and female red-shanked and gray-shanked doucs at the EPRC during July, August, October, and November 2005 and April and May 2006. We collected postural and locomotor data from 9 adult red-shanked doucs (3 females and 6 males), and 8 adult gray-shanked doucs (3 females and 5 males). We used instantaneous focal individual sampling (Altmann 1974) and bout sampling to record positional behavior and substrate type simultaneously. The use of the 2 sampling methods together allows construction of a data set in which one can address questions concerning behavioral patterns that are typical and those that are relatively rare, but perhaps equally important in terms of the overall repertoire of the species. Bout sampling methods provide the best measure of total behavioral frequencies: therefore, we provide only the data gleaned from the bout sampling. We assembled 21 h of observations on red-shanked doucs and 20 h of observations on gray-shanked doucs, with instantaneous samples recorded at 25-s intervals. We provide a randomly selected subset of the data, encompassing 1044 observations, approximately equally distributed between red-shanked doucs (571 observations from 2 adult males and 1 adult female) and gray-shanked doucs (473 observations from 2 adult males). We did not analyze differences between males and females. Locomotor behavior is any movement that involved an individual transferring its body from one substrate to another, or across a continuous substrate. Postural behavior is any position an individual took when it was not moving on, or between, substrates (Table I). In addition, we recorded whether locomotion and postures occurred on, or across, single or multiple substrates. We used χ^2 tests of independence to evaluate whether or not frequencies of locomotion and posture differed significantly between the 2 species. We also used *G*-tests as a second measure of significance owing to the relatively small number of individuals and observations that we analyzed.

Kinematic Data Collection and Analyses

During July, August, October, and November 2005 and April and May 2006, we videotaped 6 adult red-shanked doucs (3 males and 3 females) and 4 adult

Table I Ethogram of variables we used to describe the positional behavior of the doucs at the Endangered Primate Rescue Center

I. Locomotion	
Quadrupedal	A general category used to describe any form of locomotion involving forward progression on and across one or more horizontal or oblique substrates using all limbs engaged in either a symmetrical or an asymmetrical gait, as defined by Hunt *et al*. (1996).
Suspensory	A general category used to describe any movement whereby an individual propels itself beneath one or more substrates, exhibiting a roughly orthograde trunk posture at midswing. This category includes brachiation, ricochetal brachiation, brachiating leap, flexed-elbow forelimb swing, and transfer, as defined by Hunt *et al*. (1996).
Bipedal	Forward progression on a horizontal or obliquely angled substrate whereby the body is supported and propelled by the hind limbs. This category includes bipedal walk, flexed bipedal walk, and bipedal run, as defined by Hunt *et al*. (1996).
Pull up	A suspensory behavior in which one or both forelimbs are used to pull the entire body to a substrate above. This behavior usually occurs after, or in conjunction with, a suspensory movement in which the hind limbs swing up and over a horizontal substrate, so that the individual sits on top of the substrate. This category is similar to the bimanual (or unimanual) pull-up defined by Hunt *et al*. (1996), except that the individual comes to rest in a seated position, rather than on its hind limbs,
Climb	Moving up or down a vertical or steeply inclined substrate or series of substrates in which all 4 limbs are used in a regular or irregular pattern, including flexed-elbow vertical climb, ladder climb, extended-elbow vertical climb, pulse climb, rump-first descent, sideways vertical descent, and fire-pole slide, as defined by Hunt *et al*. (1996). Although also included in the category by Hunt *et al*. (1996), neither head-first descent nor pronograde slide occurred in the doucs at the EPRC.
Leap	Movement between discontinuous supports whereby the individual uses hind limb propulsion to cross a gap. It includes pronograde leap, pumping leap, and vertical clinging leap, as defined by Hunt *et al*. (1996). Although also included in the category by Hunt *et al*. (1996), neither hind limb-forelimb suspensory leap nor hind limb suspensory leap was performed by doucs at the EPRC.
II. Posture	
Sit parallel	The trunk and hind limbs are parallel to the substrate, with the trunk orthograde and ischia and hind resting on the same substrate. The forelimbs often rest on the individual's flexed hind limb (usually forearm resting on knee), or at its side, upon the substrate upon which the hind feet and ischia rest. From a purely postural perspective, thi category is similar to the flexed or extended-hind limb sit categories defined by Hunt *et al*. (1996), and both hip and knee joints may be extended or flexed.
Sit perpendicular	The trunk and hind limbs are perpendicular to the substrate, with the trunk orthograde. For the doucs at the EPRC, this posture typically incorporates multiple substrates, with the individual ischia resting on one substrate while their feet grasp or rest on another, and the knee joint may be either extended or flexed 20–40°. The forelimbs tend to either rest at the individual's side, or grasp the substrate on which the ischia rest. From a purely postural perspective, this category is similar to the flexed or extended-hind limb sit categories defined by Hunt *et al*. (1996), and both hip and knee joints may be extended or flexed.
Sit parallel suspend	Same as sit parallel, with either one or both hands to hold the substrate overhead, such that the axillary angle between the torso and humerus is ≥90°. This category is similar to the category sit/forelimb suspend defined by Hunt *et al*. (1996).
Sit perpendicular suspend	Same as sit perpendicular with either one or both hands holding the substrate overhead, such that the axillary angle between the torso and humerus is ≥90°. This category is similar to the category sit/forelimb suspend defined by Hunt *et al*. (1996).
Suspend	Use of one or both forelimbs to hang from a substrate and encompassing the subcategories within the category forelimb-suspend defined by Hunt *et al*. (1996).

Table I (continued)

Prone	Lying on ventrum. May involve the use of a single or multiple substrates. This category includes sprawl, as defined by Hunt *et al*. (1996), except that, for doucs, the belly hangs free between substrates when they lie across multiple substrates.
Supine	Lying on dorsum. May involve the use of a single or multiple substrates and is similar to the category supine lie defined by Hunt *et al*. (1996).

gray-shanked doucs (2 males and 2 females), and 5 adult white-cheeked gibbons (3 males and 2 females) at the EPRC. We captured data in the EPRC enclosures on subjects engaging in arm-swinging between variably-oriented, rigid, bark-covered branch handholds *ca*. 5 cm in diameter. Per the methods of Stevens (2003) and Stevens *et al*. (2006a, b), we positioned handheld camcorders (Sony, model DSC-HC42 NTSC) to capture lateral views of the subjects, placing recording devices at a sufficient distance to reduce parallax, 5 m from their path of movement. We optimized frame rates to catch rapid movements by splitting interlaced video fields to achieve 60 Hz and used the highest shutter speeds possible in each of the variably lit settings to reduce motion blur.

We defined swing as any locomotor sequence involving body support by a single forelimb during uninterrupted forward progression. It is distinguished from intermittent locomotion (involving locomotor sequences that are interrupted in their forward progression) or suspensory posture (nonlocomotor behaviors involving forelimb support). Whereas continuous brachiation (bimanual progression not interrupted by the use of hind limbs for propulsion) characterized most gibbon sequences, doucs typically incorporated forelimb suspension into more variable locomotor sequences.

For each taxon, we imported video clips of horizontally progressing swings (*Nomascus*: $n=10$; *P. nemaeus*: $n=10$; *P. cinerea*: $n=5$) into Peak Motus (version 5.0), identifying a series of kinematic points (Fig. 1). We included both males and females for each species ($n=2$ swings per individual of *Nomascus*; $n=2$ swings per male and $n=3$ per female of *P. nemaeus*; $n=2$ swings for one male and $n=1$ for all other individuals of *P. cinerea*). To facilitate meaningful comparisons across species of differing body segment lengths and travel speeds, we quantified differences in forelimb and trunk postures via forelimb angle —the angle between the *y*-axis, or vertical and a straight line connecting imaginary points approximating the humeral greater tubercle and the lateral aspect of the 5th metacarpal— and trunk angle: the angle between the *y*-axis and a straight line connecting 2 points representing the sagittal axis of the trunk as viewed by a camera placed perpendicular to the path of motion, i.e., lateral view (Fig. 1). We digitized kinematic points at the following standardized locomotor events: forelimb initial contact, the first frame in which the hand made contact with the support; mid-swing, the instant when the forelimb segment was parallel with the *y*-axis; and forelimb release, the last frame in which the hand was in contact with the support. Means and standard deviations for angular comparisons are in Table II. Data on individual segment kinematics across the entire swing interval are the subject of a more comprehensive kinematic analysis.

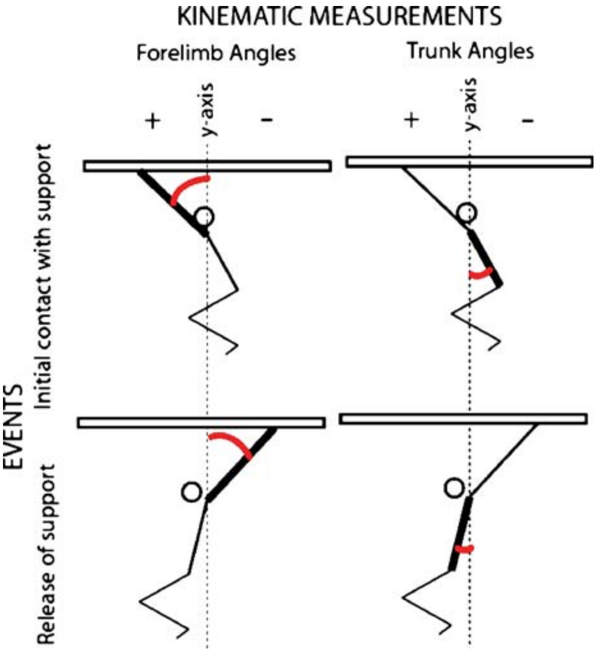

Fig. 1 Schematic of the angular kinematic variables we examined. (**a**) Forelimb angle: the angle between the forelimb segment and a vertical line). We defined the forelimb segment via a straight line connecting imaginary points approximating the humeral greater tubercle and the lateral aspect of the 5th metacarpal. (**b**) Trunk angle: the angle between the trunk segment and a vertical line). We defined the trunk segment via a straight line representing the upper and lower torso connecting imaginary points representing the ipsilateral humeral greater tubercle and femoral greater trochanter, respectively.

Results

Behavioral Results

Though the positional behavioral repertoire of doucs is more variable than that of gibbons, both *Pygathrix nemaeus* and *P. cinerea* at the EPRC regularly use bimanual locomotion. There is no statistically significant difference in pattern of locomotion. However, our results suggest that *Pygathrix cinerea* may be more suspensory than *P. nemaeus*, whereas *P. nemaeus* engages in slightly higher frequencies of leaping (Fig. 2a). Both χ^2 and *G*-test results indicate a significant difference in pattern of postural behavior ($p<0.01$). *Pygathrix nemaeus* sat with one or both abducted forelimbs grasping an overhead support more frequently during the use of multiple substrates (sit perpendicular), whereas *P. cinerea* utilized the postures more during the use of single substrates (sit parallel). Both species prefer orthograde above-branch resting positions in which the sagittal plane is perpendicular to the long axis of the support (Fig. 2b). Such postures occurred 39% of the time in *Pygathrix*

Table II Forelimb and trunk angles at initial contact with the support (FC) and at release of contact with the support (R)

	Pygathrix nemaeus		*P. cinerea*		*Nomascus*	
	Mean (*n*=10)	SD	Mean (*n*=5)	SD	Mean (*n*=10)	SD
FLA FC	41.89	6.66	36.02	1.22	40.01	6.66
FLA R	–43.11	8.92	–37.97	4.81	–45.67	4.62
TrA FC	–47.58	25.34	–57.55	5.63	–38.65	20.30
TrA R	15.58	11.87	17.19	10.74	9.81	16.04

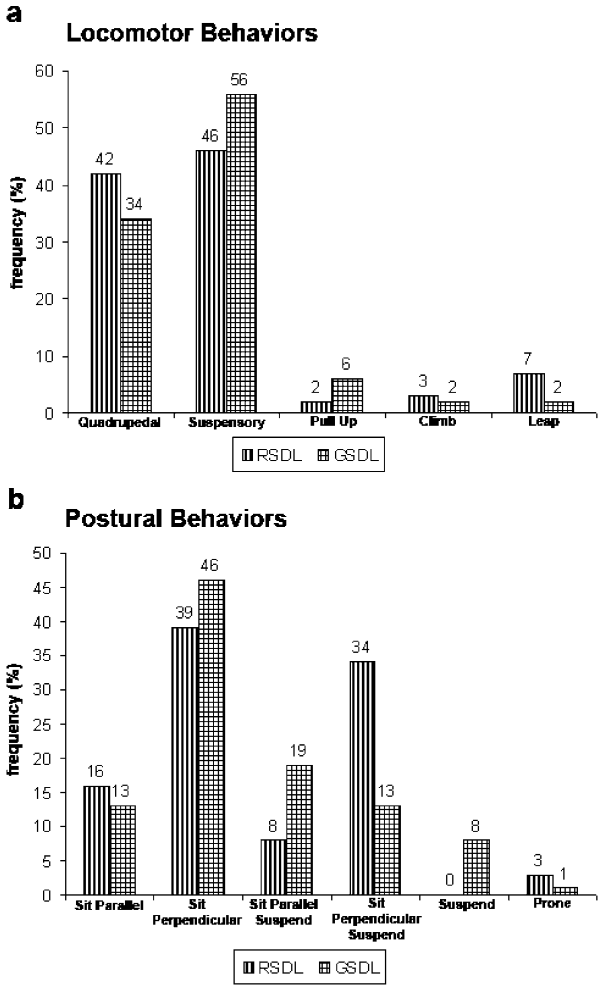

Fig. 2 Comparison of frequencies of locomotor (**a**) and postural (**b**) behaviors in red-shanked (*Pygathrix nemaeus*) and gray-shanked (*P. cinerea*) doucs at the Endangered Primate Rescue Center (EPRC). RSDL, red-shanked doucs; GSDL, gray-shanked doucs.

nemaeus and 46% of the time in *P. cinerea*. One may attribute the preference in resting posture to the fact that doucs sitting at a perpendicular orientation to the substrate tended to take advantage of multiple substrates for support, whereas resting with the long axis parallel to the branch was typically associated with the use of a single substrate (Fig. 2b). Though we interpret the results with caution because they are based on a relatively small number of bouts from a few individuals, our results corroborate the findings of Byron and Covert (2004). Both studies indicate that suspensory locomotion encompasses nearly half of the locomotor repertoire of red-shanked doucs, and we also suggest that gray-shanked doucs engage in forelimb suspension for a substantial proportion of time.

Kinematic Results

Forelimb and trunk angles at initial contact and release are in Fig. 3 for both species of *Pygathrix* and for *Nomascus*. Though gibbons typically use more continuous

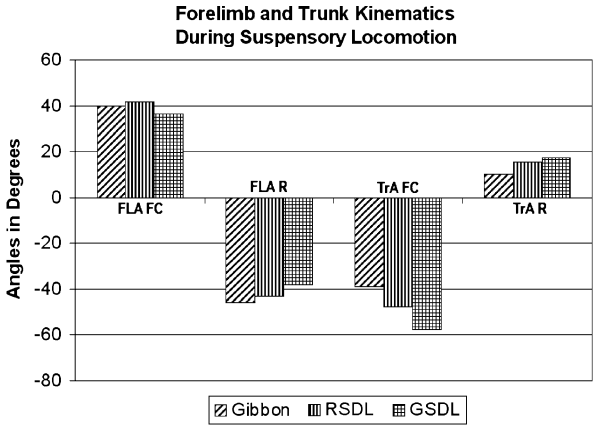

Fig. 3 Kinematic comparison of forelimb and trunk angles in doucs (*Pygathrix nemaeus* and *P. cinerea*) and gibbons (*Nomascus leucogenys*) at the Endangered Primate Rescue Center (EPRC). FLA FC, forelimb angle at first contact; FLA R, forelimb angle at release; TrA FC, trunk angle at first contact; TrA R, trunk angle at release. Note that as depicted in Fig. 1, positive angles occur when the forelimb or trunk segment extends in advance of the *y*-axis, whereas negative angles occur when the forelimb or trunk segment extends behind the *y*-axis. Standard deviations are reported in Table II.

brachiation in their locomotor bouts, mean forelimb angles at initial contact and release are remarkably similar among gibbons and doucs, averaging 36–42° for all 3 species at initial contact, and between -38° and -46° at support release (Table II). Trunk orientation tended to be on average >10˚ less vertical at initial contact in the doucs (Table II), perhaps owing to their frequent use of quadrupedal sequences directly before or after a forelimb suspensory event, but all species were highly variable in this measure (Table II). Notably, doucs are also capable of continuous bimanual locomotion, as we observed on several occasions. However, such behavior is far less typical for doucs than the more variable locomotor sequences. We included kinematic data for both males and females of each species (n=2 swings per 5 individuals of *Nomascus,* including 3 males and 2 females; n=2 swings for each of 2 males and n=3 for each of 2 females of *Pygathrix nemaeus*; n=2 swings for 1 male and n=1 for each other individual of *P. cinerea*, including an additional male and 2 females), but we view the results as preliminary until a more expansive kinematic sample is available.

Discussion

Our behavioral data support previous research by Byron and Covert (2004), Covert *et al*. (2004) and Workman and Covert (2005), which documented that doucs engage in higher frequencies of suspensory behavior than recorded for any other colobine. *Colobus polykomos, Piliocolobus badius*, and *P. verus* rely primarily on quadrupedal, leaping, and climbing behaviors, with suspensory locomotion accounting for none (*C. polykomos* and *P. verus*) or only a relatively small portion (3.3–4.9% of all locomotor observations for *C. badius*) of their repertoire (McGraw 1996). Morbeck (1977, 1979) and Gebo and Chapman (1995) showed that *Colobus guereza* engages in suspensory behaviors <2% of the time. *Presbytis melalophos* rarely engage in suspensory behaviors, and *Trachypithecus obscurus* does not use suspension. Instead, both colobines use quadrupedal and leaping behaviors most often, much like their African conspecifics (Fleagle 1978). In some cases, the frequencies of suspensory locomotion in *Pygathrix* equal or exceed those of *Ateles*. For example, Byron and Covert (2004) reported 46% for *Pygathrix*, whereas Fleagle and Mittermeier (1980) reported ≤38.6% for *Ateles*.

Kinematically, both red-shanked and gray-shanked doucs at the EPRC are capable of adopting suspensory forelimb postures similar to those exhibited by lesser apes. The behaviors are reflected in morphological features of the forelimb, wherein doucs often diverge slightly from other colobines in the direction of hominoids (Byron and Covert 2003; Covert *et al*. 2004; Wright *et al*. 2007). For example, doucs have the highest intermembral index, the second highest brachial index, and the most gracile humerus of all colobines (Covert *et al*. 2004). In addition, they have the highest forelimb/vertebral ratio, hand/vertebral ratio, and hand/foot ratio of any colobine. Complementing the indicators of elongation in each of the forelimb segments are more subtle anatomical features including a slightly more spherical humeral head and a slightly shorter olecranon than those of most other colobines. However, in contrast with the continuous bimanual locomotor sequences gibbons use, both red-shanked and gray-shanked doucs tend to incorporate forelimb suspensory behaviors seamlessly into other types of forward progression, often interspersing an arm-swing between quadrupedal strides. The findings from our kinematic analyses, combined with previous morphometric analyses, suggest that there may be important habitat constraints that impose similar performance for different morphologies of doucs and gibbons. Alternatively, the findings suggest that doucs are true brachiators, albeit slower, than gibbons.

EPRC gray-shanked doucs exhibit slightly higher frequencies of arm-swinging locomotion and suspensory postures than those of red-shanked doucs. Both *Pygathrix* spp. prefer to rest in orthograde postures with their sagittal plane perpendicular to the primary arboreal support and with the forelimbs or hind limbs positioned across multiple additional substrates. The position makes sense when one considers that these sizeable primates are leaf-eaters and must utilize the relatively unstable, small-branch environment to acquire their food. Avis (1962) discussed the utility of suspensory postures for exploiting small, flexible supports, arguing that suspensory behaviors may have evolved in response to selection for the use of such environments to avoid competition with other species that were restricted to more stable parts of the arboreal environment. Grand (1972) noted that whereas macaques and many other quadrupedal primates can exploit food items in the terminal branch setting, suspensory adaptations enable certain primates to exploit the flexible, fine-branch environment more efficiently and to gain access to foods that may be more difficult or energetically expensive for quadrupedal species to obtain.

Throughout their range in eastern Laos, eastern Cambodia, and Vietnam, doucs share their habitats with a host of other primate species. In Vietnam, doucs overlap in home range with other leaf-eating species and macaques (*Macaca*). Red-shanked doucs in central Vietnam are sympatric with Hatinh langurs (*Trachypithecus laotum hatinhensis*). Annamese silver langurs (*Trachypithecus germaini*) are sympatric with both gray-shanked and black-shanked doucs (*Pygathrix cinerea* and *P. nigripes,* respectively). In some areas, red-shanked and gray-shanked douc ranges overlap

(Nadler *et al*. 2003). Some of the forested habitat used by the primates of Vietnam and throughout much of Southeast Asia is on steep, limestone karst outcrops hosting communities exhibiting high levels of endemicity (Clements *et al*. 2006). Competition for resources within the restricted areas may help to provide a mechanism to explain the development of a suspensory repertoire in some of the Asian folivores. Leaf-eating primates that now inhabit Vietnam underwent 2 major adaptive radiations: a larger-bodied group exhibiting more suspensory adaptations (the *Pygathrix-Rhinopithecus* clade) and a relatively smaller-bodied group demonstrating more terrestrial tendencies, i.e., the *Trachypithecus* group. *Rhinopithecus* exhibits terrestrial behavior, and *R. avunculus* uses suspensory locomotion (Le Khac Quyet, *pers. comm*.; HHC and KAW, *pers. obs*.). In contrast, *Pygathrix*, which are highly suspensory (Byron and Covert 2004), also use terrestrial substrates on occasion (T. Nadler, *pers. obs*.). Suspensory capabilities within the odd-nosed group may have been selected for as the larger forms moved into subsets of a shared habitat that included a fine-branch environment. As Grand (1972) noted, the ability to use suspensory postures and locomotion, particularly in larger forms, may have given some primate species an edge in exploiting the nutrients in a terminal branch environment. We suggest that folivory, perhaps in combination with frugivory, and large body size may have acted in concert to select for suspensory adaptations in the douc/snub-nosed monkey clade. Pan *et al*. (2004) argued that the diet of *Mesopithecus pentelicus* may have been more similar to that of modern odd-nosed species. If true, and given the emerging revelation regarding the locomotor and postural capabilities of some of the extant odd-nosed species, our data may help to clarify models of the positional behavior of extinct forms, such as *Mesopithecus.* Ultimately, a fuller understanding of differences in habitat use and substrate preference among Southeast Asian leaf monkeys will require further investigations into their natural behavior and habitat use.

Conclusions

As in any research on agile arboreal primates, visibility of the study subjects is always an issue, a requirement made particularly demanding by the conditions necessary for conducting the kinematic aspects of our study. In addition, the endangered status of the subjects is a major challenge in gaining access to them outside of their limited natural habitat. Finally, finding a common vocabulary to embrace the questions of both positional behavior and locomotor kinematics proved more challenging than we had anticipated. Despite our enthusiasm for adopting a synthetic approach, numerous refinements in data collection and management in the field setting were critical in the early stages of the project to examine successfully positional behavior in conjunction with locomotor kinematics.

Conditions at the EPRC allow us to work together to unite naturalistic methods of behavioral observation with kinematic experimental protocols to engage in a synthetic approach that one can use to quantify and to describe a broad range of locomotor and postural behaviors.

Our work represents an integrated approach to the study of primate positional behavior that utilizes both naturalistic and experimental methods in a controlled field setting. The combination of methods allows us to fine-tune our descriptions of behavior and to quantify more accurately posture and locomotion, as well as substrate use. Our work at the EPRC has allowed us to generate more informed hypotheses of how patterns of posture and locomotion may benefit the species in the wild. The information may also allow us to identify the structural aspects of the environment that are most critical for the welfare of leaf-eating monkeys and ultimately provide an important contribution to the efforts to conserve them.

Both behavioral and kinematic data must next be obtained from wild populations of doucs, including black-shanked doucs (*Pygathrix nigripes*), to delve deeper into the adaptive significance of suspensory behavior and variation in positional repertoires within the genus. Research focusing on the positional behavior and habitat use of closely related but relatively understudied species such as Tonkin snub-nosed monkeys (*Rhinopithecus avunculus*), and perhaps also proboscis monkeys (*Nasalis larvatus*) and pig-tailed langurs (*Simias concolor*), will provide an important addition to the data set and will illuminate further our understanding of the diverse and highly endangered radiation of primates.

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