

Kinetic and kinematic patterns of arm-swinging in the red-shanked douc langur (*Pygathrix nemaeus*)

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Summary

Douc langurs (genus *Pygathrix*) are special amongst the Asian colobines because of their ability to use arm-swinging as a form of locomotion. While arm-swinging has been studied extensively in gibbons, very few studies have explored movements during arm-swinging in the douc langurs. This study uses video-recordings and force plate analysis to explore the mechanics of arm-swinging in the red-shanked douc langurs (*Pygathrix nemaeus*), and determine whether the biomechanics of arm-swinging in the red-shanked douc langur are similar to other arm-swinging species. All data was collected from two adults at the Endangered Primate Rescue Center in Cuc Phuong National Park, within the Nho Quan District of Ninh Binh Province. Arm-swinging in the red-shanked douc langur appeared to be remarkably similar to patterns observed in other arm-swinging primates. The force traces collected from the red-shanked douc langurs are largely consistent with movements of a simple pendulum, with the exception of relatively large side-to-side movements. Shoulder, elbow, and wrist movements also closely matched what has been observed in other species, despite high variability in values reported for the wrist. These findings support the idea the mechanics of arm-swinging are highly conserved between taxa, and might indicate that there are limited functional solutions to the challenges associated with below branch locomotion. It is possible that selection may drive species that use below branch locomotion to a mechanical optimum similar to the movements of simple pendulum.

Nghiên cứu về động học, động lực học của kiểu di chuyển “tung người bằng chi trước” ở loài Voọc chà vá chân nâu (*Pygathrix nemaeus*)

Tóm tắt

Voọc chà vá (*Pygathrix*) tương đối đặc biệt trong số những loài voọc ở Châu Á vì khả năng di chuyển theo kiểu tung người kiểu vượn. Kiểu di chuyển này được nghiên cứu rất kỹ ở các loài Vượn, nhưng còn ít ở những loài chà vá. Nghiên cứu này sử dụng các bản ghi video tập tính và dụng cụ phân tích lực để khám phá cơ chế cơ học của kiểu di chuyển tung người kiểu vượn ở loài chà vá chân nâu. Nghiên cứu cũng xác định yếu tố sinh cơ học của kiểu di chuyển này giống và khác như thế nào so với các loài linh trưởng khác. Số liệu được thu thập trên hai cá thể trưởng thành được nuôi tại trung tâm cứu hộ thú linh trưởng Cúc Phương, Ninh Bình, Việt Nam.

Kết quả cho thấy, kiểu di chuyển bằng tay tung người kiểu vượn ở loài chà vá chân nâu tương đối giống với mô hình được quan sát ở những loài linh trưởng có cùng kiểu di chuyển. Phân tích về lực cho thấy, sự vận động của loài chà vá chân nâu rất phù hợp với sự chuyển động của con lắc đơn, ngoại trừ có những chuyển động sang hai bên. Vai, cẳng tay và cổ tay lúc di chuyển tương đối giống với những loài linh trưởng khác có cùng kiểu di chuyển, ngoại trừ cổ tay có sự biến thiên lớn hơn. Phát hiện này ủng hộ ý tưởng rằng cơ chế cơ học của kiểu di chuyển bằng tay tung người kiểu vượn thường rất bảo thủ giữa các taxa, và có thể những hạn chế chức năng liên quan đến kiểu di chuyển dưới cành cây. Chọn lọc tự nhiên có thể đã khiến những loài di chuyển dưới cành cây chọn cơ chế tối ưu theo kiểu chuyển động của con lắc đơn.

Introduction

Since the time of Jones (1916), numerous studies have investigated both the mechanics of arm-swinging, and its broader role in the context of human evolution (Avis, 1962; Bertram 2004; Chang et al., 2000; Churchill et al., 2013; Fleagle et al., 1981; Michilsens et al., 2009; 2010; 2011; Stern, 1975; Stern & Oxnard, 1973; Stern & Susman, 1983; Usherwood, 2003). Arm-swinging is a form of suspensory locomotion in which the forelimbs bear more than half of the body's weight, and may or may not be accompanied by significant trunk rotation, and/or the use of a prehensile tail as an additional means of support (Hunt et al., 1996; Turnquist et al., 1999; Byron & Covert, 2004; Schmitt et al., 2005; Workman & Covert, 2005; Wright et al., 2008).

Traditionally, arm-swinging has been studied in the new world atelids (Turnquist, 1975; Turnquist et al., 1999; Schmitt et al., 2005) and the old world hylobatids (Swartz et al., 1989; Chang et al., 2000; Usherwood, 2003; Bertram, 2004; Michilsens et al., 2009; 2010; 2011), and from these species we assume that arm-swinging requires extensive morphological adaptations [e.g., a well-developed scapular spine, long forearms relative to humerus and body size, sagittally thickened radii, axially elongated scapulae, curved clavicles (Michilsens et al., 2009; Fleagle, 2013)]. Recent work however (Byron & Covert, 2004; Workman & Covert, 2005; Wright et al., 2008; Su & Jablonski, 2009; Bailey & Pampush, 2015) has demonstrated that this may not be the case.

First described by Byron & Covert (2004), and later corroborated by Workman & Covert (2005) and Wright et al. (2008), is the unexpected ability of the red-shanked douc langur to commonly [46%; (Byron & Covert, 2004)] engage in arm-swinging locomotion. This observation is surprising, because anatomically *P. nemaesus* closely resembles other phylogenetically related Asian colobines [but see Su & Jablonski (2009) and Bailey & Pampush (2015)], and shows few of the anatomical similarities with other arm-swinging primates. While the remarkable ability for *P. nemaesus* to use arm-swinging to locomote is well-known, a detailed mechanical analysis to understand the proficiency of this locomotion is currently absent. Additionally, because only preliminary kinematics (Wright et al., 2008) and no kinetics have been collected, it is difficult to determine whether the mechanics of arm-swinging observed in *P. nemaesus* are similar to what has been reported in other arm-swinging primates.

According to values reported by Wright et al. (2008) shoulder movements during arm-swinging in *P. nemaesus* at touchdown and lift-off closely match levels of protraction and retraction that have been reported during arm-swinging in *Ateles* and *Hylobates* (Turnquist et al., 1999; Michilsens et al., 2011; Tripp et al., 2015). Unfortunately, angular movements of the wrist and elbow, as well as overall patterns of limb loading have not been explored during arm-swinging in *P. nemaesus*. Kinematic studies of elbow movements during arm-swinging in *Ateles*, *Lagothrix*, and *Hylobates* all demonstrate substantial elbow extension throughout support phase (Turnquist, 1975; Turnquist et al., 1999; Michilsens et al., 2011; Tripp et al., 2015). Patterns of wrist movement however are much more variable. Based on data from Tripp et al. (2015), it appears that *Hylobates* maintains a neutral wrist position throughout support phase, while *Ateles* demonstrates substantial radial and ulnar deviation. In contrast, Turnquist (1975) reported that *Ateles* shows little wrist motion throughout support phase, and maintains neutral wrist positions similar to *Hylobates*.

Kinetic studies of arm-swinging primates have been rare, and only one (Chang et al., 2000) has collected single limb forces. Chang et al. (2000) collected multi-axial force data during continuous-contact arm-swinging from a freely moving gibbon (*Hylobates lar*) on an instrumented runway. From these data Chang et al. (2000) determined that (1) vertical forces displayed a single peak pattern with maximum vertical force (Vpk) reaching approximately 1.8% of body weight; (2) as the limb makes contact with the support it applies a propulsive force to the substrate during the first half of support phase, followed by a braking force throughout the remainder of support phase; and (3) mediolateral forces were low and inconsistent (a pattern usually suggesting little movement outside the parasagittal plane). The patterns above are consistent with movements of a simple pendulum, and it is possible, as suggested by Chang et al. (2000), that all arm-swinging primates solve the mechanical challenges of suspensory locomotion through similar kinematic and kinetic strategies. Currently, the data necessary to address this hypothesis is unavailable. This study provides essential information on the variation of kinematic and kinetic gait patterns during arm-swinging across primate

taxa, and provides previously unknown data concerning the mechanical patterns of arm-swinging in *P. nemaeus*.

Materials and Methods

Kinematic and kinetic gait data were collected during arm-swinging from captive *P. nemaeus* at the Endangered Primate Rescue Center in Cuc Phuong National Park, following the protocols approved Duke's Institutional Animal Care and Use Committee (IACUC protocol # A270-11-10). All animals were adults and were clear of any pathologies or gait abnormalities (Table 1). The methods used here have been described extensively elsewhere (Ishida et al., 1990; Demes et al., 1994; Turnquist et al., 1999; Schmitt & Hanna, 2004), and will only be summarized below.

Table 1. Animal subjects used in the study, and the number of strides analyzed for each individual.

Subject	Sex	Average body weight	Number strides analyzed for kinetic portion of study	Number strides analyzed for kinematic portion of study
Individual 1	Male	9.23 kg	8	14
Individual 2	Female	8.16 kg	6	14

Forelimb forces were collected while animals moved below an instrumented runway measuring approximately 3.66 m in length and 3.1 cm in diameter. The instrumented portion of the runway consisted of an AMTI multi-axis force plate (MC3A-100) attached to a section of dowel (45.72 cm) measuring the same diameter as the rest of the runway. This instrumented section was mounted in the middle of the runway flush with, but separated by a small gap from, the rest of the runway. Force plate output was sampled at 1200 Hz, and imported, summed, and processed using AMTI-NetForce software, and then filtered (Butterworth, 30 Hz) and analyzed using MATLAB. From these data ten variables were calculated for each limb: (1) Vpk force; (2) peak propulsive force (Ppk); (3) peak braking force (Bpk); (4) peak medial force (Mpk); (5) peak lateral force (Lpk); (6) propulsive impulse (PI); (7) braking impulse (BI); (8) net horizontal impulse (HI); (9) medial impulse (MI); and (10) lateral impulse (LI). Additionally, the timing at which Vpk, Ppk, Bpk, and the propulsive to braking transition was also recorded within each stride. The PI, BI, MI, and LI are measured as a specific area under the force-time curve in the horizontal (PI and BI) and mediolateral (MI and LI) component of the substrate reaction force. The HI provides a means for differentiating the overall braking or propulsive role of the limb during particular locomotor behaviors (Demes et al., 1994). The overall HI for each limb was calculated by subtracting the BI from the PI. Positive HI values indicate a net propulsive limb while negative values indicate a net braking limb (Kimura et al., 1979; Ishida et al., 1990; Demes et al., 1994). In regards to mediolateral forces, data was standardized so all medially directed forces are represented as negative values, and all laterally directed forces are represented as positive values. In order to make comparisons between subjects of differing body masses, Vpk, Ppk, Bpk, Mpk, and Lpk forces are given in multiples of body weight (bw), and PI, BI HI, MI, and LI are given in body weight seconds (bws).

Prior to all trials, animals were weighed, and forces for each day of trials were normalized to the body weight recorded for that day. The animals were videotaped during trials from a lateral view using a GoPro camera (Hero 3+ Black Edition; GoPro, San Mateo, CA) modified with a Back-Bone Ribcage (Ribcage v1.0; Back-Bone, Ottawa, ON), which allows the GoPro cameras to be outfitted with interchangeable lenses and eliminates image distortion inherent to the camera. All videos were recorded at 120 fields/second. For each step, the subject's velocity was calculated by digitizing a point on the subject's head and determining the time necessary to cross a known distance marked on the runway. Only strides in which the animal was traveling in a straight path and not accelerating or decelerating (i.e., steady-state locomotion) were selected for analysis. Steady-state locomotion was determined by calculating the instantaneous velocity between subsequent video frames throughout the entire stride, and then using regression analysis to determine whether velocity changed throughout the stride. Only strides in which no change in velocity was detected were used for subsequent analyses. Additionally, only handholds with single-limb contacts on the plate were analyzed.

From video recording, the position of the shoulder, elbow, and wrist were collected over the course of support phase (i.e., when the limb is in contact with the substrate). The resulting x-y coordinate data was used to track angular movements in the shoulder, elbow, and wrist. All angular movements were measured in degrees (°). Shoulder angles were measured relative to the vertical axis of the body [i.e., when the arm passed directly above the head this was considered the neutral position (0°)]. Angles greater than 0° represent shoulder protraction, while angles less than 0° represent shoulder retraction. Elbow angles always reflect elbow flexion, where 180° represents maximum elbow extension. Wrist angles were measured based on the position of the wrist relative to the point-of-contact with the support and the elbow. Neutral position (180°) was defined as the point in which the wrist was in line with the point-of-contact and the elbow. Due to tendency of *P. nemeus* to grab the support using pronated hand-holds, a pattern also observed by Byron & Covert (2004), angles greater than 180° represent ulnar deviation, while angles less than 180° represent radial deviation. All limb angles were digitized using DLT Dataviewer (Hedrick, 2008) in MATLAB.

Results

Kinetic data

In total, 14 strides were selected for kinetic analysis. Summary statistics are presented in Table 2. Patterns of force data largely represent what is expected for an animal moving similarly to a simple pendulum (Fig. 1). The vertical force component was characterized by a single peak that occurred on average at 42.06% ± 6.69% of support phase. The horizontal component consisted of a propulsive force that occurred early in support phase as the limb first made contact with the support. This propulsive force reached its maximum on average at 24.04% ± 8.01% of support phase, and subsequently decreased until the propulsive to braking transition, which occurred on average at 49.35% ± 7.26% of support phase. Throughout the remainder of the stride the limb exerted a braking force, which reached its maximum on average at 73.03% ± 7.78% of support phase. The mediolateral force component was dominated by medially directed forces, although these were generally low in comparison to the vertical and horizontal forces (Table 2).

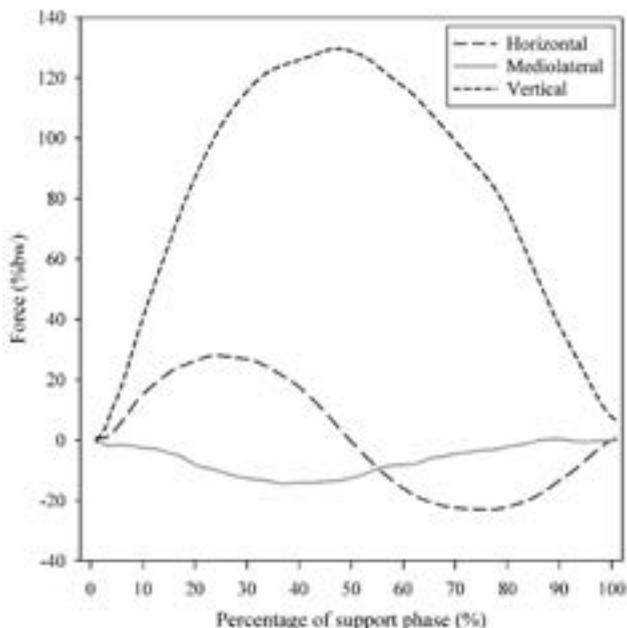


Fig.1. Mean force trace for all strides collected in this study. Positive values in the horizontal force component indicate propulsive forces, while negative values indicate braking forces. Positive values in the mediolateral force component indicate laterally directed forces, while negative values indicate medially directed forces. All data is presented as a percentage of the body weight (% bw).

Table 2. Summary statistics for velocity and kinetic variables analyzed in this study.

Velocity (m/s)*	Propulsive peak (%bw)	Braking peak (%bw)	Medial peak (%bw)	Lateral peak (%bw)	Vertical peak (%bw)	Propulsive impulse (%bws)	Braking impulse (%bws)	Net horizontal impulse (%bws)	Medial impulse (%bws)	Lateral impulse (%bws)
1.10 ± 0.24	30.34 ± 6.80	-26.69 ± 12.83	-19.39 ± 7.17	7.47 ± 4.91	130.87 ± 20.55	7.65 ± 4.16	-7.29 ± 5.66	0.36 ± 3.97	-6.06 ± 3.16	1.06 ± 1.18

*Velocity determined from 28 strides, while all other kinetic variables were collected from 14 strides.

Kinematic data

In total, 28 strides were selected for kinematic analysis. Summary statistics are presented in Table 3. Shoulder movements demonstrate relatively equal levels of protraction and retraction, and the shoulder reached its neutral position approximately midway throughout support phase (Fig. 2A). Elbow movements during arm-swinging in *P. nemaeus* are characterized by somewhat flexed positions at touchdown, followed by extension until late in support phase at which point the joint was flexed again (Fig. 2B). The wrist was ulnarly deviated early on at touchdown and was subsequently radially deviated throughout the remainder of support phase (Fig. 2C).

Table 3. Summary statistics for shoulder, elbow, and wrist movements at regular intervals from touchdown (TD) to the end of support phase support phase. All angles were measured in degrees (°).

Joint	TD	10%	20%	30%	40%	50%	60%	70%	80%	90%	100%
Shoulder	50.34 ± 10.43	42.69 ± 8.48	30.77 ± 11.36	16.16 ± 9.51	6.80 ± 6.50	-2.53 ± 5.42	-9.50 ± 6.13	-17.67 ± 6.66	-30.22 ± 7.34	-39.68 ± 7.52	-50.59 ± 8.23
Elbow	168.56 ± 9.90	171.03 ± 6.83	171.41 ± 4.57	173.89 ± 4.50	173.55 ± 3.39	173.09 ± 3.76	172.62 ± 4.89	171.88 ± 4.83	168.15 ± 4.81	168.47 ± 6.44	166.13 ± 7.28
Wrist	191.27 ± 10.85	187.78 ± 14.49	178.41 ± 15.189	172.59 ± 18.48	170.05 ± 17.90	165.21 ± 16.61	159.63 ± 16.00	153.90 ± 17.22	153.79 ± 16.60	152.53 ± 21.31	152.26 ± 20.15

Discussion

The goal of this study was to explore the kinematics and kinetics of arm-swinging in *P. nemaeus* to determine whether patterns of movement observed in this species match what has been reported from other arm-swinging primates. Kinetic patterns largely reflect what is expected for an animal moving similarly to a simple pendulum. The force traces collected from *P. nemaeus* are characterized by single vertical peak occurring approximately at mid-support, a propulsive force occurring within the first half of support phase, and a braking force occurring during the latter portion of support. Mediolateral forces were higher than expected for a simple pendulum, which should be zero. This finding supports earlier findings by Byron & Covert (2004) that demonstrate that *P. nemaeus* uses some side-to-side movement during arm-swinging. A similar pattern has also been reported during arm-swinging in *Lagothrix* (Schmitt et al., 2005).

Overall, kinetic patterns collected during arm-swinging from *P. nemaeus* closely match those of *Hylobates* described by Chang et al. (2000), but with some exceptions. The average Vpk force reported by Chang et al. (2000) during continuous contact arm-swinging in *Hylobates* was 1.8% of body weight. This value is higher than what was observed in *P. nemaeus*. The reason for this may simply be a result of higher speed strides collected by Chang et al. (2000), which could have significant effects on the magnitude of substrate reaction forces (Demes et al., 1994). It is also possible that active forelimb flexion commonly observed during arm-swinging in gibbons (Fleagle, 1974; Michilsens et al., 2011) could have resulted in the higher Vpk forces reported by Chang et al. (2000). Additional differences can be seen when comparing mediolateral forces. *Pygathrix nemaeus* displayed medially directed forces during arm-swinging close to 20% of body weight. In contrast, *Hylobates* exerted only minimal mediolateral forces. This finding suggests that *Hylobates* may be more effectively replicating the movements of simple pendulum.

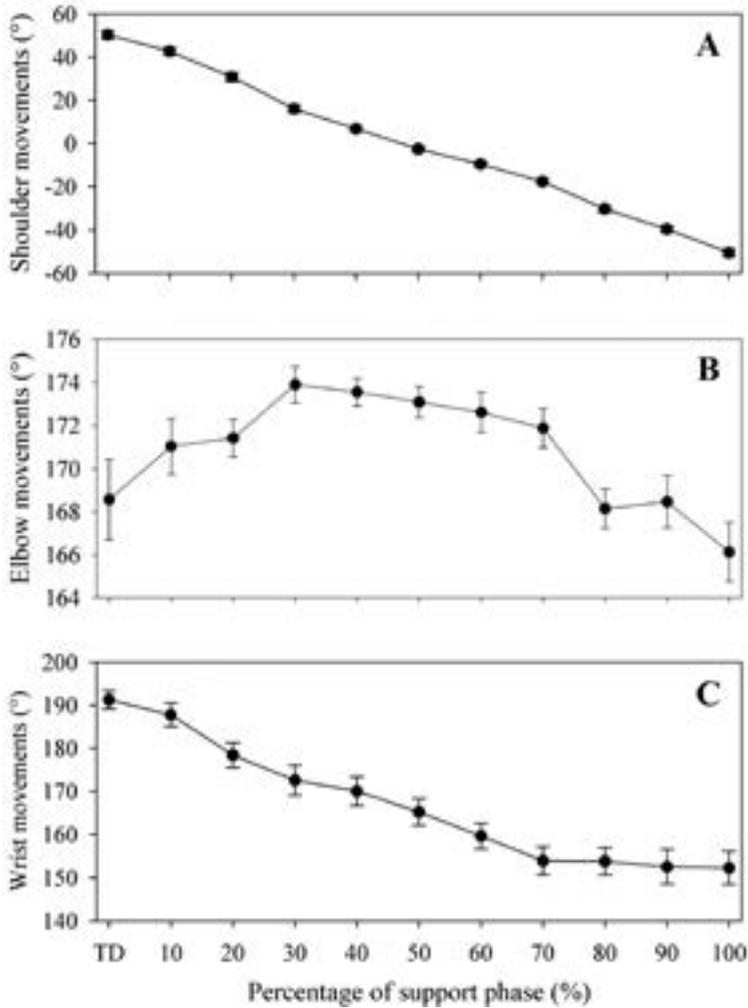


Fig.2. Patterns of shoulder (A), elbow (B), and wrist (C) movements from touchdown (TD) to the end of support phase during arm-swinging in *Pygathrix nemaeus* (mean and standard error). All angular measurements are reported in degrees. Shoulder angles are reported relative to the neutral axis of the body (0°). Angles greater than 0° represent shoulder protraction, while angles less than 0° represent shoulder retraction. Elbow angles always reflect elbow flexion, where 180° represents maximum elbow extension. Wrist angles are reported relative to the neutral position of the wrist (180°). Wrist angles greater than 180° represent ulnar deviation, while angles less than 180° represent radial deviation.

Shoulder movements closely match what has been observed in other arm-swinging primates (Turnquist et al., 1999; Michilsens et al., 2011; Tripp et al., 2015). At touchdown the shoulder is protracted beyond the neutral position, and is subsequently retracted throughout the remainder of the stride. The levels of protraction and retraction observed in *P. nemaeus* are approximately equidistant from the neutral position demonstrating substantial angular excursion throughout support phase. The consistency of this kinematic pattern across arm-swinging primates likely represents a mechanical necessity that is required effectively to swing the body below branches. This idea of mechanical necessity is further supported by the anatomical convergence observed in scapular morphology between distantly related arm-swinging primates (Su & Jablonski, 2009; Bailey & Pampush, 2015).

The patterns of elbow movements also closely match what has been reported for other arm-swinging primates (i.e., the elbow remains extended throughout the stride, and some flexion occurs at the beginning and end of support phase) (Turnquist, 1975; Turnquist et al., 1999; Michilsens et al., 2011; Tripp et al., 2015). This finding is not surprising because longer pendulum lengths (i.e.,

extended elbows) are thought to result in overall more efficient arm-swinging [but see Usherwood (2003)]. The ability to extend the elbow joint is largely determined by the length of the olecranon process of the ulna. Shorter olecranon processes allow for a greater range of extension at the elbow joint, but at the cost of muscular mechanical advantage (a trait necessary for terrestrial and arboreal quadrupeds). Su & Jablonski (2009) demonstrate that *P. nemaeus* have relatively short olecranon processes compared to other phylogenetically related colobines, with morphology more similar to other suspensory species. The short olecranon process, and the functional consequence of greater elbow extension, may represent a feature selected for in all suspensory species.

Overall patterns wrist movements during arm-swinging in *P. nemaeus* were consistent across strides and individuals, although angular values were variable. As first reported by Byron & Covert (2004), and confirmed in this study, *P. nemaeus* grabs the support with pronated handholds. This means that as *P. nemaeus* grabs onto the support the wrist is first ulnarly deviated, and subsequently radially deviated throughout the remainder of the stride. This results in substantial movement in the radio-carpal and ulnar-carpal joints. Patterns for other arm-swinging species are less clear and highly variable. This variability and lack of data make it difficult to infer patterns of wrist movements across species. What is clear is all arm-swinging species appear to have significant mobility within the wrist allowing for substantial range-of-motion. Some species that commonly adopt suspensory postures lack an ulna-pisiform and ulnotriquetral articulation, and have an increased expansion of radiocarpal joint surfaces. Additionally, certain arm-swinging primates possess a rotary mid-carpal region where the scaphoid is capable of rotating around the medial capitate. Together, these traits are thought to reflect adaptations for high joint mobility that allow species to move fluidly and rapidly below branches (Cartmill & Milton, 1977; Mendel, 1979). It is possible that *P. nemaeus* shares similar anatomical features within its wrist.

Conclusions

Pygathrix nemaeus represents a fascinating species for studying locomotor transitions and convergence. Due to its close phylogenetic position to the hominoids, this species represents an ideal model for how an anatomically unspecialized arboreal quadruped may have made the transition to specialized suspensory locomotion. From the data collected in this study it is clear that the kinematic and kinetic patterns observed in *P. nemaeus* are remarkably similar what has been reported in other arm-swinging primates. This finding might indicate that there are limited functional solutions to the challenges associated with arm-swinging, and selection may drive species to a mechanical optimum similar to a simple pendulum.

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