

LOCOMOTION OF THE RED-SHANKED DOUC LANGUR (*PYGATHRIX
NEMAEUS*) IN THE SON TRA NATURE RESERVE, VIETNAM

A Dissertation

by

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ABSTRACT

This study aims to compile data on the locomotor behavior of the red-shanked douc langur (*Pygathrix nemaeus*). This dissertation focused on establishing the historical context for primate locomotion studies and provides a brief introduction to the odd-nosed monkeys, of which *Pygathrix* is a member. Furthermore, this dissertation contributes locomotor and some anatomical data relating to the arm-swinging capabilities of the red-shanked douc langur.

Landmark data was used to identify elements of scapular shape to infer locomotor behaviors. I used shape data on the scapula of the douc langurs to identify if the three species of *Pygathrix* share a similar scapula shape. There was no statistically significant difference in scapular shape between the three species, thereby lending some support that all are likely moving in similar ways. I also used landmark data to compare *Pygathrix* (all three species) to quadrupeds and brachiators and found *Pygathrix* to be significantly different from both. Landmark data was also used to calculate the straight-line distance between the distal most portion of the acromion process and the center most point of the glenoid fossa to see if this distance could predict locomotor behaviors. For species that routinely use their arms for locomotor purposes (i.e. brachiators, quadrupeds, and arm-swingers) there was a significant difference in distance between the groups. When incorporating bipedal individuals, there was less of a significant effect.

In addition I looked at behavior data from the Son Tra Nature Reserve in Da Nang City, Vietnam to identify elements of wild locomotion. I looked at body size

characteristics to determine if heavier individuals were arm-swinging more or less than lighter individuals. This study showed that in fact, the lightest individuals (juveniles) used arm-swinging the most, followed by sub-adults, adult females, adult females carrying babies, and then adult males. Finally, I identified environmental variables and how those variables correlate with the red shanked douc's locomotion. The results of this study indicated that doucs prefer to arm-swing in old-growth forest, in the main canopy, and on horizontal and medium sized substrates.

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CHAPTER I

INTRODUCTION AND LITERATURE REVIEW

1.1. Introduction to Primate Locomotion

Primate locomotion is often divided into discrete categories, despite most scholars agreeing that locomotor behavior often lies along a spectrum. With this in mind, locomotor designations do provide a framework to organize the existing literature and provide a scheme from which future research can be built (Napier and Napier 1967). In general, there are four major locomotor categories: [1] leaping, [2] quadrupedalism, [3] brachiation, and [4] bipedalism; which are sometimes further broken down into sub categories (e.g., arboreal quadrupedalism, terrestrial quadrupedalism, etc.) (e.g. Fleagle 2013; Napier and Napier 1967). These locomotor classifications create a way for deductive science to be used on the existing and forthcoming data (Rose 1973).

The goal of this classification scheme is to eliminate sources of confusion where different sets of characteristics were used to define similar terms (Rose 1973). Prior to the 1960s, most anthropoid primates were categorized into three main groups: quadrupeds, brachiators, and semibrachiators (Ashton and Oxnard 1963). Ashton and Oxnard (1964b) noted that these categories did not encompass all of the locomotor variability observed in the wild and from this tried to develop a more robust classification scheme. They did note, however, that the major groups (brachiators, semibrachiators, and quadrupeds) would be retained based on function of the forelimb alone, despite the spectrum of observed locomotion.

The term semibrachiation was put forth to replace the phrase ‘occasional brachiation’ (Napier and Davis 1959) that was used to describe intermittent overhead brachiation that was proposed for the extinct Miocene hominoid *Proconsul*. Later works (Napier 1961; Napier 1963) also used this term, and it was popularized in the seminal work by Napier and Napier (1967). Old World semibrachiation is defined as “during leaping the arms reach out ahead of the body to grasp a handhold or to check momentum. Hand over hand progression is seldom seen. Quadrupedalism is common” (Napier and Napier 1967:388). The semibrachiator designation largely fell out of use after it became clear that many colobines, and in particular African colobines, rarely, if ever, used brachiation (e.g. Hunt et al. 1996a; Mittermeier and Fleagle 1976; Ripley 1975; Rose 1973).

1.2. Introduction to Odd-Nosed Monkeys

The subfamily Colobinae is a diverse group of primates found throughout Africa and Asia that typically move through an arboreal environment quadrupedally and they also engage in a great deal of leaping (Davies and Oates 1994). Colobinae is split into two geographically isolated tribes, Colobini (African) and Presbytini (Asian) (Fleagle 2013). Presbytini (genera *Semnopithecus*, *Presbytis*, *Trachypithecus*, *Simias*, *Nasalis*, *Rhinopithecus*, and *Pygathrix*) encompasses a clade known as the odd-nosed monkeys. The odd-nosed monkeys consist of four genera (*Nasalis*, *Pygathrix*, *Rhinopithecus*, and *Simias*) that are found in Southeast Asia (Su and Jablonski 2008). These primates have little overlap in their geographic ranges, and are united by a genetic, evolutionary history and each taxa have distinct nasal morphologies (Liedigk et al. 2012). The nasal

morphology of each genus in the clade is quite distinctive, though some are more similar than others. The proboscis monkey (*Nasalis larvatus*) is the most sexually dimorphic colobine—males are twice the size of females on average (Fleagle 2013). The males are characterized by an extremely large proboscis, while the females have a much shorter upturned nose (Fleagle 2013). The female proboscis monkey nose is very similar to their sister taxa, *Simias concolor*, which also have a short upturned nose (Tilson 1977). The douc langurs (*Pygathrix* spp.) and the snub-nosed monkeys (*Rhinopithecus* spp.) have extremely reduced, upturned noses, but the snub-nosed monkeys have arguably the shortest noses (Fleagle 2013).

The odd-nosed monkeys are estimated to have split from other Presbytini members around 7.28 – 6.90 Ma (Liedigk et al. 2012; Sterner et al. 2006). *Rhinopithecus* spp. is the first member of the clade to have split from the other odd-nosed monkeys (mtDNA = 7.28 Ma, nucDNA = 6.77 Ma) (Liedigk et al. 2012). *Pygathrix* is estimated to have diverged between 6.63 Ma (mtDNA) and 5.99 Ma (nucDNA) from *Nasalis* and *Simias*, which then split from each other approximately between 1.92 Ma (mtDNA) and 1.12Ma (nucDNA) (Liedigk et al. 2012). The genus *Pygathrix* consists of three species, the red-shanked douc langur (*Pygathrix nemaeus*), the grey-shanked douc langur (*Pygathrix cinerea*), and the black-shanked douc langur (*Pygathrix nigripes*). Of the douc langurs, the black-shanked douc is the most basal taxon based on molecular data (Roos and Nadler 2001). *Pygathrix cinerea* and *P. nemaeus* split from *P. nigripes* between 2.5 Ma (mtDNA) and 1.58 Ma (nucDNA) (Liedigk et al. 2012). Subsequently, *P. nemaeus* and *P. cinerea* split around 0.66 Ma (nucDNA) (Liedigk et al. 2012).

Nasalis larvatus is found in riverine and coastal forests of Borneo (Fleagle 2013). At least one study notes the use of brachiation, as well as leaping, walking, and climbing in a captive setting (Hollihn 1973). *Nasalis* is known to exhibit quadrupedalism, climbing, and leaping (Falk and Byram 2000). While little information has been published regarding their use of arm-swinging behaviors, they are known to swim across rivers as an anti-predator strategy (Yeager 1991).

The genus *Rhinopithecus* contains five species distributed throughout east and south Asia (Fleagle 2013). *Rhinopithecus bieti* (Yunnan snub-nosed monkey) is known to use climbing extensively in arboreal settings and in one study (Isler and Grüter 2006) the author suggests the forelimb morphology of *R. bieti* to be a reflection of climbing rather than arm-swinging. An additional study of *R. bieti* found the locomotion of adults to consist primarily of walking, climbing, and jumping (Wu 1993). Bleisch et al. (1993) noted *R. brelichi* use brachiation occasionally for up to three ‘steps’ at a time. Similarly, adult males of *Rhinopithecus avunculus* (the Tonkin snub-nosed monkey) were observed using arm-swinging behaviors infrequently (5.23% of the time) (Le Khac Quyet 2014).

Simias is exceptionally under-represented in the locomotor literature to the point that no study has focused exclusively on the locomotion of *Simias concolor*. For example, Falk and Byram (2000), describe *Simias* simply as a quadruped. Similarly, in Tilson (1977) thorough investigation of the pig-tailed langur’s social organization, he describes them as merely having an arboreal lifestyle similar to Patas monkeys (*Erythrocebus patas*), while also noting that leaping is not commonly used.

Pygathrix was placed into the locomotor category of Old World semibrachiator because of their Colobinae status, given that their locomotion was unknown in the wild (Napier and Napier 1967). Wild-based studies on the douc langurs are largely dominated by feeding ecology and conservation studies (e.g. Dinh Thi Phuong Anh et al. 2010; Ha Thang Long 2007; Hoang Minh Duc et al. 2009; Phiapalath 2009; Rawson 2009; Timmins and Duckworth 1999; Ulibarri 2013) and few have investigated their locomotion. The locomotion of *Pygathrix* has been extensively studied at the Endangered Primate Rescue Center (hereafter, EPRC) (Byron and Covert 2004; Granatosky 2015; Workman and Covert 2005; Wright et al. 2008). The EPRC houses numerous colobines in enclosures which allows for comparative study of Southeast Asian colobine locomotion.

Field studies on doucs have rarely focused on locomotion. Some initial observations on the population of red-shanked douc langurs living on Son Tra mountain in Da Nang, Vietnam noted that “large males, when disturbed, would brachiate back and forth in full view” (Van Peenen et al. 1971:134-135). This observation is in contrast to subsequent studies that only briefly noted that douc langurs travel quadrupedally in the trees, in single file groups, along established paths (Lippold 1998). Rawson (2009) completed a study on the socioecology of the black-shanked douc langur and found suspensory behavior to be used 10% of the time by males, and 3.7% of the time by females during locomotion.

1.3. Organization of Dissertation

To fully understand the discrepancies in the captive and (limited) wild studies of the locomotor behavior in the doucs, this dissertation will attempt to answer the following

questions: first, despite the differences in frequencies of arm-swinging in the *Pygathrix* genus, do the doucs have a scapular shape that is consistent across the genus? Second, does the scapula of the doucs resemble that of other quadrupeds or brachiators? Third, is it possible to predict locomotion based on the distance the acromion process projects past the glenoid fossa? Fourth, do the doucs arm-swing in the wild with frequencies consistent with their captive behavior and is this influenced by body size? Fifth, are there environmental variables that influence arm-swinging behaviors among the douc langurs? In the subsequent chapters we attempt to answer these questions.

CHAPTER II

INTRAGENERIC SHAPE VARIATION OF THE DOUC LANGUR (*PYGATHRIX* SPP.) SCAPULA*

2.1. Introduction

The douc langurs (genus *Pygathrix*) are Asian colobines (tribe Presbytini) that make up one of the four genera of the ‘odd-nosed monkeys’ (Fleagle 2013; Groves 2001). Relative to other colobines, these primate genera (*Rhinopithecus*, *Simias*, *Nasalis*, and *Pygathrix spp.*) are united by a distinct nasal morphology, a high intermembral index (90+), and sometimes a larger body size (Table 1) (Fleagle 2013; Groves 2001). It is estimated that the odd-nosed clade split from other Presbytini members approximately 6.9 Ma followed by *Pygathrix*, which diverged from the other odd-nosed taxa approximately 6.63 Ma (Liedigk et al. 2012; Sterner et al. 2006). Today there are three species of douc langurs, *Pygathrix cinerea* (grey-shanked douc), *Pygathrix nemaeus* (red-shanked douc), and *Pygathrix nigripes* (black-shanked douc) (Roos and Nadler 2001).

Douc langurs are smaller than *Rhinopithecus* and *Nasalis* and are slightly larger than *Simias* (Table 1) (Delson et al. 2000; Smith and Jungers 1997). Like most other colobines, douc langurs exhibit a largely folivorous diet, multi-chambered stomachs, relatively long tails, high molar shearing crests, and reduced thumbs (Fleagle 2013). As is

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suggested by their common names, the red, gray, and black-shanked douc langurs are phenotypically distinguished by the coloration of their hind-limbs. The douc langurs inhabit evergreen and semi-evergreen forests throughout Southeast Asia with little overlap in their geographic ranges (Lippold and Vu Ngoc Thanh 2016). *Pygathrix nigripes* is found in southern Vietnam and eastern Cambodia, *P. cinerea* is found in the central highlands of Vietnam, and *P. nemaesus* is found in northern Cambodia, east-central Laos, and north-central Vietnam (Rawson et al. 2008; Vu Ngoc Thanh et al. 2008a; Vu Ngoc Thanh et al. 2008b).

Table 1. Weights of Asian colobines. Averages taken from Delson et al. (2000), Fleagle (2013), and Smith and Jungers (1997).

Species	Male (kg)	Female (kg)
<i>Semnopithecus schistaceus</i>	23.587	14.829
<i>Nasalis larvatus</i>	21.3	10.53
<i>Semnopithecus ajax</i>	19.959	12.701
<i>Rhinopithecus roxellana</i>	18.16	11.95
<i>Rhinopithecus bieti</i>	17.96	10.94
<i>Semnopithecus hector</i>	17.237	13.154

Table 1 Continued

Species	Male (kg)	Female (kg)
<i>Semnopithecus entellus</i>	17.018	11.516
<i>Semnopithecus priam</i>	16.783	8.845
<i>Rhinopithecus avunculus</i>	16.5	8.13
<i>Rhinopithecus brelichi</i>	14.5	NA
<i>Pygathrix cinerea</i>	11.55	8.45
<i>Pygathrix nigripes</i>	11.03	8.35
<i>Pygathrix nemaus</i>	10.93	8.22
<i>Trachypithecus ebenus</i>	10.3	NA
<i>Simias concolor</i>	9.16	6.84
<i>Trachypithecus delacouri</i>	9	7.7
<i>Trachypithecus poliocephalus</i>	8.75	7.35
<i>Trachypithecus hatinhensis</i>	7.5	7.2
<i>Trachypithecus francoisi</i>	7.48	7.14
<i>Trachypithecus crepusculus</i>	6.9	6.4
<i>Presbytis thomasi</i>	6.775	6.74
<i>Presbytis femoralis</i>	6.26	6.19
<i>Presbytis hosei</i>	6.18	5.599
<i>Presbytis potenzani</i>	6.153	6.42
<i>Presbytis frontata</i>	5.682	5.67

Table 1 Continued

Species	Male (kg)	Female (kg)
Presbytis rubicunda	5.682	6.137

The taxonomy of the genus *Pygathrix* has recently been in flux. Prior to 2001 the regional diversity in douc langurs was often regarded as intra-specific variation and a number of researchers classified all as members of the species *Pygathrix nemaeus* (Nadler 1997). *Pygathrix nemaeus* was first described by Linnaeus in 1771. Milne-Edwards (1871) later designated the black-shanked douc as the species *Semnopithecus nigripes*. Finally, the grey-shanked douc was named by Nadler [1997] as *Pygathrix nemaeus cinerea*. In 2001, Mitochondrial DNA findings supported the reorganization of *Pygathrix* into the currently recognized set of three species, elevating the subspecies into species (Groves 2001; Roos and Nadler 2001). The undisputed findings of Roos and Nadler (2001) is one of the bases for the current three species phylogeny. *Pygathrix nigripes* is estimated to have diverged 1.69 – 1.31 Ma (from other *Pygathrix spp.*) followed by *P. cinerea* and *P. nemaeus* at 0.66 Ma (Liedigk et al. 2012). Additionally, Roos and Nadler [2001] noted phylogenetic structure in the genus, finding *P. nigripes* to be the most basal taxon (molecularly) and *P. nemaeus* and *P. cinerea* to be sister taxa.

In addition to the taxonomy, the locomotor classification of the douc langurs has also been under recent revision. Historical literature placed the douc langurs into the

‘semibrachiator’ locomotor category but indicated *Pygathrix* seldom exhibited arm-swinging behaviors (Napier and Davis 1959; Napier and Napier 1967). The term semibrachiator was initially put forth on the basis of musculoskeletal studies of some colobines (e.g. *Presbytis*, *Rhinopithecus*, *Nasalis*, *Colobus*) (Ashton and Oxnard 1963; Ashton and Oxnard 1964a; Ashton and Oxnard 1964b). In addition to the musculoskeletal studies, it was observed that these colobines would leap then use their forelimbs to grasp handholds or check momentum (Napier 1963). In their classic work, Napier and Napier (1967) included *Pygathrix* in the category “Old World Semibrachiator” (Table 2). A study of *Rhinopithecus bieti* (sister taxa to *Pygathrix*) found *R. bieti* to use climbing extensively and the authors suggested that the forelimb morphology of *Rhinopithecus* is actually a reflection of climbing rather than arm-swinging (Isler and Grüter 2006). Another study found *R. bieti* to use semibrachiation only on rare occasions (Wu 1993). Additional work on *Rhinopithecus avunculus* found these monkeys to use arm-swinging behaviors in low frequencies, about 5.23% of the time (Le Khac Quyet 2014).

Table 2. Old World semibrachiators classification adapted from Napier and Napier (1967).

Category	Sub-type	Genera
Quadrupedalism	Slow climbing type	<i>Arctocebus, Loris, Nycticebus, Perodicticus</i>
	Branch running and walking type	<i>Aotus, Cacajao, Callicebus, Callimico, Callithrix, Cebuella, Cebus, Cercopithecus, Cheirogaleus, Chiropotes, Lemur, Leontideus, Phaner, Pithecia, Sanguinus, Saimiri, Tupaia</i>
	Ground running and walking type	<i>Macaca, Mandrillus, Papio, Theropithecus, Erythrocebus</i>
	New World semi-brachiation type	<i>Alouatta, Ateles, Brachyteles, Lagothrix</i>
	Old World semi-brachiation type	<i>Colobus*, Nasalis, Presbytis, Pygathrix, Rhinopithecus, Simias</i>
Brachiation	True brachiation	<i>Hylobates, Symphalangus, Nomascus</i>
	Modified brachiation	<i>Gorilla, Pan, Pongo</i>

Unlike the other odd-nosed colobines, the red-shanked douc and the grey-shanked douc have been regularly observed engaging in brachiation and forelimb suspension in captivity at the Endangered Primate Rescue Center (EPRC) in Cuc Phuong National Park in Northern Vietnam (Byron and Covert 2004; Workman and Covert 2005; Wright et al. 2008). Byron and Covert (2004) found suspensory behavior to make up 46% of all the red-shanked douc langurs' locomotor bouts within the EPRC. Similarly, Wright et al. (2008) found suspensory behavior to encompass nearly half of the douc langurs locomotor repertoire and found a gradient in the frequency of suspensory behaviors between two species of doucs (*P. nemaus*, 46%; *P. cinerea*, 56%). The suspensory locomotor behavior expressed by *Pygathrix* in the EPRC has also been recently observed in wild groups of black-shanked doucs (Rawson 2009; Tran Van Bang et al. 2011). Some wild postural data of red-shanked doucs has also reported the use of suspensory and brachiation behaviors (Ulibarri 2013). The infrequently observed semi-brachiation behavior in their sister taxa combined with information about the age of the clade suggests a relatively recent locomotory shift to the semi-brachiator status in *Pygathrix*.

The scapula is an important component to forelimb use and therefore its morphology is dramatically influenced by locomotor behavior, including brachiation and presumably semi-brachiation (Ashton and Oxnard 1964a; Green 2013; Larson 1993). Scapular skeletal markers indicative of brachiating behaviors include a well-developed scapular spine, a cranially oriented and relatively shallow glenoid fossa, and narrow supra- and infraspinous fossae (Ashton and Oxnard 1964a; Larson 1993; Michilsens et al. 2009).

Ashton and Oxnard (1964a) speculate that the scapular features of a semibrachiator should fall in an intermediary position between true brachiators and quadrupeds. A previous study recorded scapular indices of the odd-nosed monkeys and found this grade to exhibit a morphology similar to the great apes and the atelines—groups thought to be adapted (at least in part) to brachiation (Su and Jablonski 2008). Though in the last 15 years there have been a handful of behavioral studies supporting the semibrachiator category, few morphological studies have been conducted (Byron and Covert 2004; Covert et al. 2004).

This study is an investigation into the scapular shape diversity within the genus *Pygathrix*. Though Wright et al. (2008) found differences in suspensory behavior between *P. nemaeus* and *P. cinerea*, the relatively small nature of the behavioral differences suggests they are unlikely to have an effect on scapular form. We hypothesize that the genus *Pygathrix* shares a common gross scapular morphology, presumably one consistent with observed locomotor behaviors despite minor variations in semi-brachiation frequencies [Wright et al. 2008]. Given the uniform scapular shape, and the observations by Rawson (2009), it is likely *P. nigripes* is likely at least occasionally arm-swinging, which is an important inference given *P. nigripes*' basal status within the genus. Here we present preliminary data on the gross scapular shape of the douc langurs.

2.2. Methods

To assess the scapular shape within the genus *Pygathrix* a Microscribe G2X (Immersion Technologies San Jose, California) was used to record landmark data on 35 specimens (Table 3). Following Young (2008) 17 landmarks were recorded at bony junctions on the scapula (Figure 1, Table 4). These landmarks are ideal because they are

easily identifiable on all primate taxa and also assess the gross components of the scapula by marking all major boney intersections, protuberances, and depressions. Given the variable locomotor behavior of juvenile primates, and the underdeveloped nature of juvenile morphology, only adult specimens were used in this study (Young 2006). Specimens were measured at the EPRC, the Dalat Museum (Dalat, Vietnam), the Southern Institute of Ecology (Ho Chi Minh City, Vietnam), and the Muséum National d'Histoire Naturelle (Paris, France). Specimens were required to be mostly complete, with at least 15 landmarks present. Two *P. nigripes* specimens were broken in minor places and required imputation. Imputation estimates where missing landmarks from the incomplete specimen would be based on a reference point from a complete specimen. The first specimen that was broken required imputation for landmarks four and eight. The second broken specimen required imputation for landmark number four. All data analyses were conducted using the geomorph package in R (Adams and Otárola-Castillo 2013). Landmark data were Procrustes-transformed prior to conducting principal components analyses (PCA). A Procrustes ANOVA and a Pairwise Group ANOVA were further performed to quantitatively assess the differences among *Pygathrix spp.* scapulae.

Table 3. Species counts.

Species	N	Location/ Person Who Provided Specimens:
<i>Pygathrix cinerea</i>	14	Ha Thang Long = 2 Endangered Primate Rescue Center = 12
<i>Pygathrix nemaeus</i>	18	Muséum National d'Histoire Naturelle = 2 Endangered Primate Rescue Center = 16
<i>Pygathrix nigripes</i>	3	Dalat Museum = 1 Southern Institute of Ecology = 2

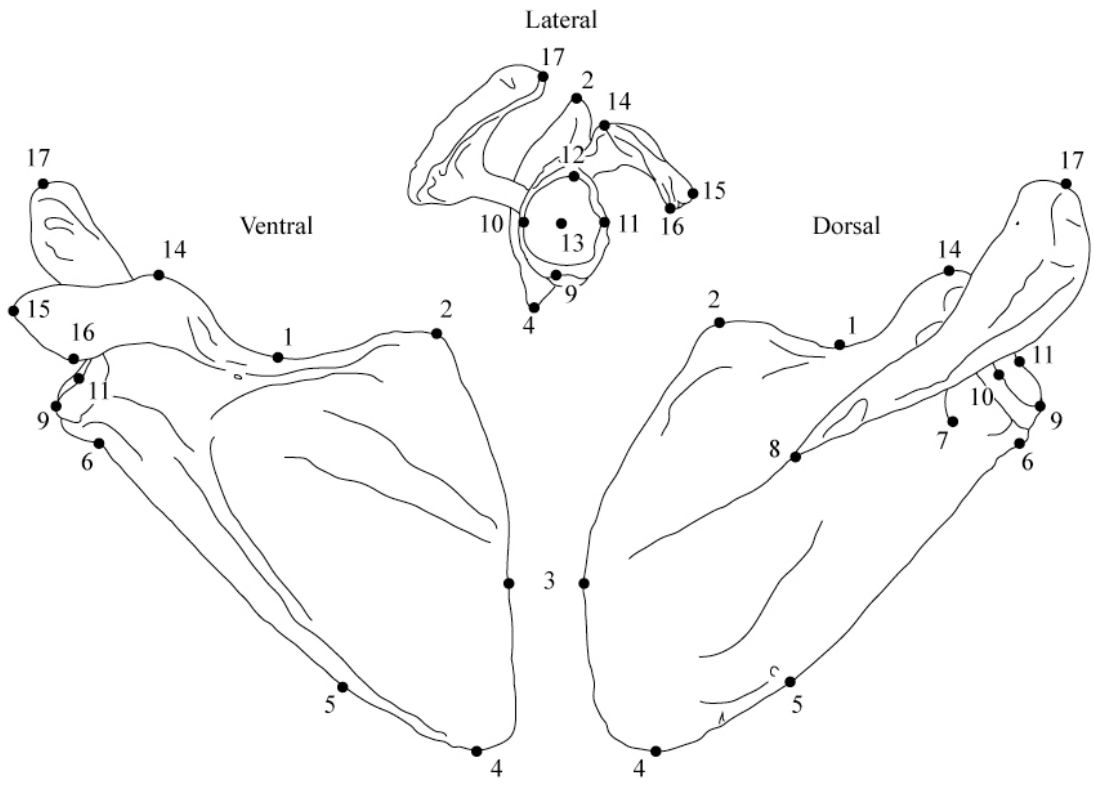


Figure 1. Landmarks used following the methods of (Young 2008).

Table 4. Landmarks used following the methods of Young (2008).

	Landmarks
1	Inferior most point of the suprascapular notch
2	Superior most point of the superior angle
3	Central most point of vertebral border and scapular spine intersection
4	Inferior most point of inferior angle
5	Superlatero corner of the teres major attachment site
6	Maximum curvature of the infraglenoid tubercle
7	Maximum curvature of the spinoglenoid notch
8	Medial extent of trapezius attachment on scapular spine
9	Most inferior extent of glenoid fossa
10	Most lateral extent of glenoid fossa
11	Most medial extent of glenoid fossa
12	Most superior extent of glenoid fossa
13	Central maximum curvature of glenoid fossa
14	Medial most portion of the coracoid prominence
15	Superior-lateral tip of the coracoid process
16	Inferior-lateral tip of the coracoid process
17	Distal-most point of the acromion process.

2.3. Results

The Procrustes ANOVA showed no significant difference ($P = 0.354$) between the three species (Table 5). Power decreases the more landmarks are considered and it is difficult to consider more than three landmarks because landmarks are multi-dimensional (Rohlf 2000). Results of the pairwise group ANOVA also showed no statistically significant difference between the taxa ($P = 0.344$) (Table 6). Principal Component (PC) one accounts for approximately 27% of the variation, PC two accounts for 15% of the variation observed in the scapula, and the first five PC scores account for approximately 68% of the overall variation (Table 7). The PCA generally shows an intermingled distribution of the species (Figure 2). *Pygathrix nigripes* has positive PC scores on the first and second axis and are therefore confined to the upper-right quadrant of the graph whereas *P. nemaeus* and *P. cinerea* are evenly distributed across PC one and two.

Table 5. Results Procrustes ANOVA

DF	SS	r^2	F	p
14	0.0151	0.0628	0.0958	0.354

Table 6. Results Pairwise Group ANOVA

DF	SS	r ²	F	<i>p</i>
14	0.0151	0.0628	0.0958	0.344

Table 7. PCA Results

	PC1	PC2	PC3	PC4	PC5
SD	0.0437	0.0327	0.0295	0.0241	0.0209
Proportion of Variance	0.2713	0.1523	0.1232	0.0825	0.0621
Cumulative Proportion	0.2713	0.4236	0.5468	0.6294	0.6916

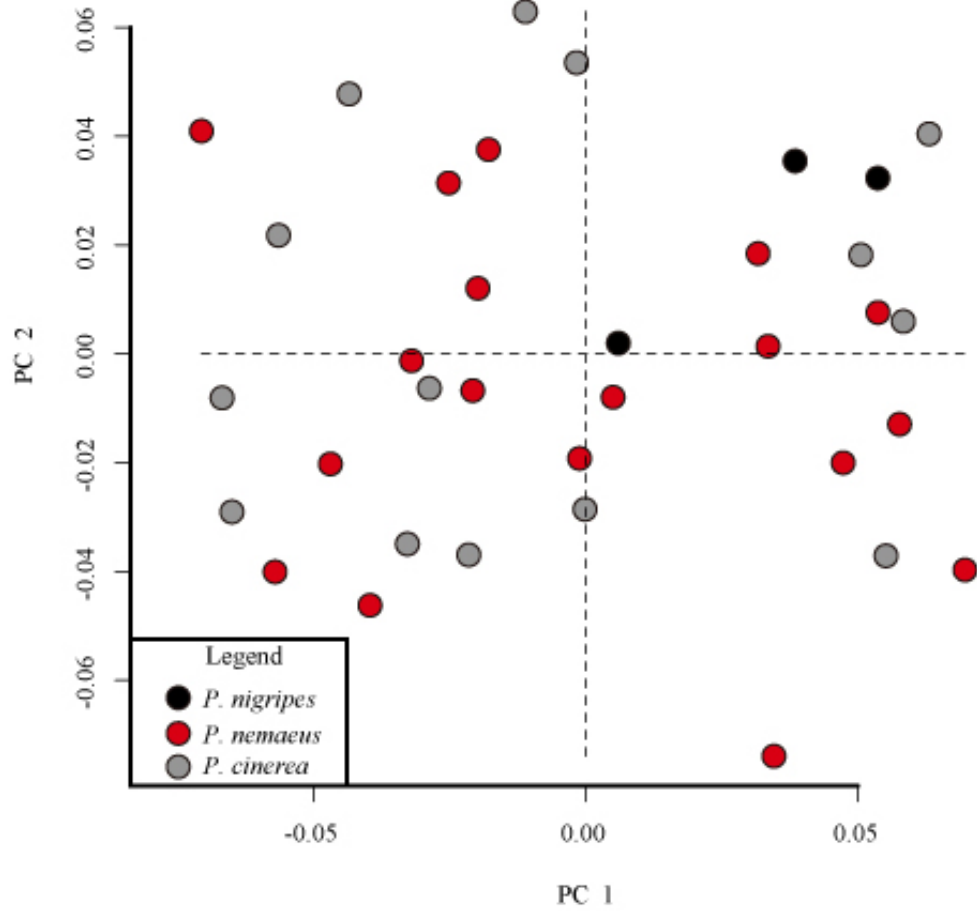


Figure 2. Principle Component Analysis of scapular shape diversity of *Pygathrix* spp.

2.4. Discussion

The results presented here provide tentative support for the hypothesis that there is no significant variability in scapular shape of the douc langurs. Due to the rarity of these primates, specimen availability is limited, particularly for *P. nigripes*. For this reason, some caution is required when interpreting these results. However, considering the overall distribution of the three taxa within the principal components analyses, as well as the results of the ANOVAs, the three taxa appear to share a similar scapular morphology. Due to these similarities, coupled with the work of Rawson (2009), we confirm that the locomotor behavior of the black-shanked douc is also that of a semibrachiator.

The douc species have virtually no overlap in their range. The grey-shanked douc is primarily found at higher elevations in the Central Highlands of Vietnam where the environment and vegetation is appreciably different (Vu Ngoc Thanh et al. 2008a). The forest in Kon Ka Kinh National Park (in the central highlands) is a lowland moist subtropical forest (Ha Thang Long et al. 2011). Grey-shanked doucs in Gai Lai Province, Vietnam are known to spend 60% of feeding time in trees that are 15 – 19.9 meters in height (Ha Thang Long 2010). In the Son Tra Nature Reserve, which hosts a population of red-shanked doucs, trees tend to be shorter (9.34 ± 3.52 meters) (Ulibarri 2013) whereas the mean height of sleeping trees for the black-shanked douc langur in the Mondulhiri Province, Cambodia was 20.83 ± 3.06 meters (Rawson 2009). The density of vegetation, tree height, and changes in elevation in these differing areas might require modifications to typical locomotor behaviors. Additionally, despite the gradient in observed frequencies

of suspensory behaviors documented by Wright et al. (2008), there was no noticeable difference in scapular shape between the red and grey-shanked douc langurs.

Increased body size is suggested to increase the proclivity towards below-branch locomotion versus above-branch locomotion (Napier and Napier 1967; Young 2003). Arboreal colobines also tend to be significantly larger than their arboreal cercopithecine cousins (Fleagle 2013), none of which are grouped into Napier and Napier's [1967] 'Old World Semi-brachiation' category (Table 2), whereas Napier and Napier (1967) classified all of the odd-nosed monkeys as semibrachiators. However, each of the odd-nosed monkey species tends to move through their environment in different ways. *Nasalis* has been observed swimming in the mangrove swamps of Indonesia in addition to the trees and *Rhinopithecus bieti* is largely terrestrial and is often found slow climbing to maneuver through the trees (Isler and Grüter 2006; Yeager 1991). Conversely, *R. avunculus* rarely comes to the ground (Le Khac Quyet 2014). We speculate that the increased body size in odd-nosed monkeys is a contributing factor to the varying locomotor patterns observed in this clade, and especially the use of brachiation and slow-climbing types of locomotion when arboreal.

2.5. Conclusion

This morphological study shows no significant variation between the scapulae of the three *Pygathrix* species. The douc langurs are a particularly understudied group of Old World monkey (Byron and Covert 2004). The studies that have been conducted on their locomotor behavior have predominantly been in a captive environment (e.g. Byron and Covert 2004; Covert et al. 2004; Workman and Covert 2005; Wright et al. 2008).

Notwithstanding the oscillating changes in taxonomy and locomotor classifications, a long-term study of the douc langur locomotor repertoire should be considered for future studies to further identify frequencies of arm-swinging and suspensory behaviors in their natural habitat. Other morphological studies of the humerus and clavicle would be especially useful, in conjunction with field studies to identify shape variability within the genus that is related to their locomotor patterns. This study also warrants an investigation of the scapular shape of semibrachiators and of the muscular morphology. It is possible semibrachiators, specifically *Pygathrix*, have a unique scapular morphology reflective of their intermediate locomotor category.

CHAPTER III
FUNCTIONAL MORPHOLOGY OF THE DOUC LANGUR (*PYGATHRIX* SPP.)
SCAPULA*

3.1. Introduction

Colobine monkeys are generally recognized to be arboreal quadrupeds with most exhibiting leaping behaviors to some extent (e.g. Fleagle 1978; Gebo and Chapman 1995; McGraw 1998b; Rose 1973). Suspensory locomotion (i.e., below branch arm-swinging and hanging) is atypical for this group (e.g. Davies and Oates 1994; Fleagle 2013) but has been intermittently observed in captive douc langurs (*Pygathrix*), first in zoos (Hollihn 1973) and, more recently, at the Endangered Primate Rescue Center (EPRC) in Cuc Phuong National Park, Vietnam, where high frequencies of forelimb suspension and arm-swinging have been reported (Figure 3) (Byron and Covert 2004; Wright et al. 2008). Douc langurs are capable of suspensory postures similar to those of gibbons (*Nomascus leucogenys*), but these postures are better described as arm-swinging, rather than true brachiation due to the slower moving suspensory, less fluid behavior exhibited by the doucs (Wright et al. 2008). Outside of the captive setting, information about douc langur locomotion, especially arm-swinging frequency data, is more limited. However, one study (Rawson 2009) has documented arm-swinging in nearly 10% of all travel bouts across all

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age and sex classes in wild black-shanked doucs (*Pygathrix nigripes*), a higher frequency than documented for other free-ranging colobines (Fleagle 1977; McGraw 1998b; Morbeck 1977; Rose 1978). While this is less frequent than what is reported for captive douc langurs, it is likely safe to infer that arm-swinging is not simply an artifact of captivity.

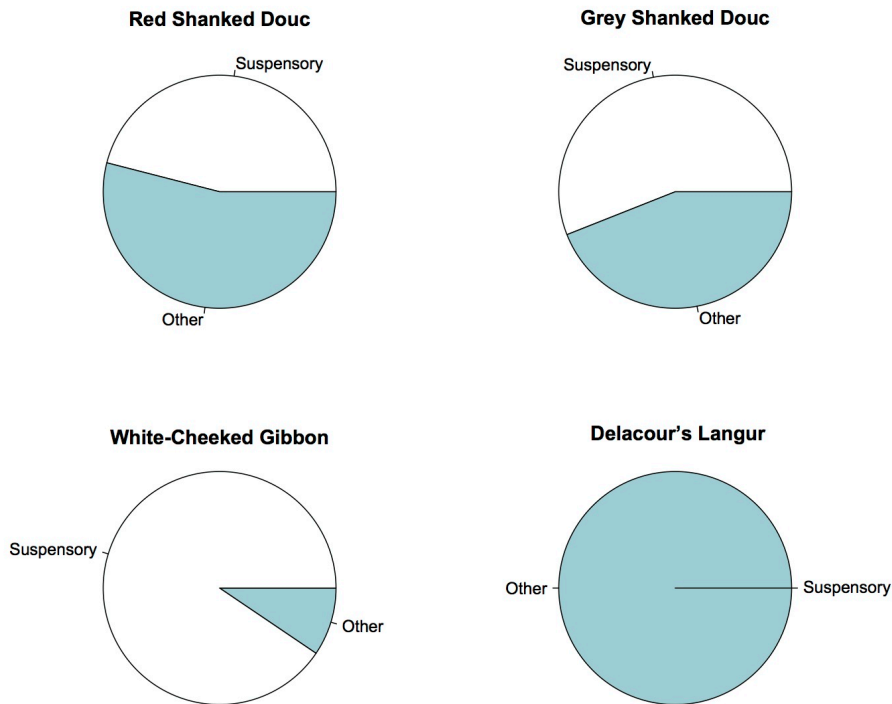


Figure 3. Amount of suspensory behavior versus other locomotor patterns observed in *Pygathrix nemaeus* (21 hours of observation), *P. cinerea* (20 hours of observation), *Nomascus leucogenys* (70 hours), and *Trachypithecus delacouri* (70 hours of observation) at the EPRC (Byron and Covert 2004; Wright et al. 2008).

Scapula shape differs between quadrupedal and brachiating primates and these differences lie along a spectrum; that is, there are no distinct differences between the groups (Roberts 1974). However, there are observable general trends in scapular form for each locomotor group. Typical quadrupeds have more laterally situated scapulae while

brachiators and suspensory primates have more dorsally placed scapulae as a result of the broader thorax found in most hominoids (Gebo 1996). The broad thorax sets the scapulae further apart and allows greater shoulder mobility (Gebo 1996). The glenoid fossa of brachiators is wider and more cranially oriented (Larson 1993), which has been proposed to be an adaptation for distributing strain more evenly across the glenohumeral joints (particularly during unimanual arm-hanging) (Hunt 1991). The orientation of the glenohumeral joint is relatively static during ontogeny and has thus been suggested to be more developmentally constrained (Green 2013). The acromion process, which articulates with the clavicle, typically projects further past the glenoid fossa in brachiators relative to arboreal quadrupeds (Larson 1993). Concomitantly, brachiator clavicles are more often elongated (Ashton and Oxnard 1964a; Jenkins et al. 1978). In suspensory primates, the acromioclavicular joint is more robust to better transfer weight from between the glenohumeral joint and the manubrium (via the clavicle) (Hunt 1991). The deltoid muscle, which attaches to and overlays the clavicle, acromion process, and humerus (Moore et al. 2002) is a shoulder rotator, abductor, flexor, and extensor (Myatt et al. 2012). This muscle is an important component of the brachiating anatomy because it envelops and stabilizes the glenohumeral joint, and is the primary shoulder abductor (a motion critical to brachiation) (Ashton et al. 1965; Jungers and Stern 1981). In addition to the deltoid, four other scapular muscles are critical for shoulder stabilization: infraspinatus, supraspinatus, teres minor, and subscapularis (the rotator cuff muscles) (Dvir and Berme 1978). These muscles are also involved in movement of the shoulder joint (Roberts 1973). The supraspinatus muscle attaches on the supraspinous fossa of the scapula and inserts on the

middle facet of the greater tubercle of the humerus. The supraspinatus assists the deltoid in arm abduction (Moore et al. 2002; Myatt et al. 2012). The origin of the supraspinatus muscle in the supraspinous fossa is quite broad in brachiators while it is comparatively long and narrow in quadrupeds (Ashton and Oxnard 1963). Because the deltoid and supraspinatus muscles contribute directly to the ability to brachiate, their attachment sites are typically more robust given the extensive use of those muscles. The other three rotator cuff muscles (infraspinatus, subscapularis, and teres minor) show no considerable differences between brachiators and quadrupeds (Ashton and Oxnard 1963).

Overall, the brachiator scapula is taller from the most superior to inferior points and more narrow across the scapular spine (Larson 1993). This narrower scapula is thought to maximize the range of rotation of the shoulder joint, thus bringing the glenoid fossa closer to a position over the center of gravity during arm-hanging. In this position, the glenoid is aligned with the spinal column so that the two elements are in the same line of action. This functions to decrease bending of the spinal column, reduce shear stress on the structure between the glenoid and spine, and more evenly distribute compressive stress on the rib cage by presenting a straighter profile of the torso (Hunt 1991). By contrast, a quadruped scapula is more laterally placed, shorter in overall height, and wider across the scapular spine. This positioning and shape function to limit the mobility of the shoulder joint and provide more stability (Larson 1993). The brachiator scapula is also generally more robust in terms of overall size and muscle attachment sites. This robusticity corresponds to the physiological cross-sectional area of the muscles of the brachiator forelimb. Greater cross-sectional area increases the maximum available force of a muscle,

which is especially important in the brachiator forelimb muscles (Anapol and Gray 2003; Fleagle 1976; Wright et al. 2008). One of the ways gibbons have adapted an efficient brachiating pattern is by distributing forelimb muscle mass at the proximal ends of the limb, keeping the majority of that muscle's mass centered near the trunk (Michilzens et al. 2009).

Observations of the douc langurs arm-swinging at the EPRC (e.g. Byron and Covert 2004) invites speculation that their scapular morphology reflects this derived—relative to other colobines—locomotor behavior. Given the differences in scapular anatomy between brachiators and quadrupeds, we predict that the douc langur scapula possesses features analogous to obligate brachiators (such as gibbons). Previous studies have used indices to measure scapular form but capture only a portion of the overall shape. For example, Su and Jablonski (2008) found that odd-nosed monkeys (*Pygathrix*, *Simias*, *Nasalis*, *Rhinopithecus*) have derived scapular morphology more similar to that of extant apes and Covert et al. (2004) found douc langurs to have a longer vertebral border of the scapula compared to the Delacour langur (*Trachypithecus delacouri*). Here we present a more comprehensive analysis of overall scapular form. We specifically aim to measure douc langur scapular morphology relative to other cercopithecoid quadrupeds and to hylobatid brachiators, and to assess their similarities and differences. Should the results indicate that *Pygathrix* scapular morphology is more similar to quadrupeds, this would suggest that the arm-swinging behaviors of the douc langurs are more facultative in nature and their scapular morphology is reflective of more habitual, quadrupedal locomotor behaviors. A more similar morphology to true brachiators (i.e., hylobatids) would suggest

selective pressures have acted on the douc langur scapula to accommodate suspensory and locomotor activities.

3.2. Methods

This research adhered to the American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates. Seventeen landmarks (Table 8, Figure 4) were collected following the methods of Young (2006; 2008) from scapulae of 100 adult individuals from 15 different species of catarrhines (Table 9) using a Microscribe G2X from Immersion Technologies (San Jose, California). The three collections that were visited for data collection were chosen based on where I could get the largest representative sample for each of the three locomotor groups; cercopithecids at Ohio State, Hylobatids at Muséum National d'Histoire Naturelle, and *Pygathrix* at the EPRC. All landmarks were recorded from the dorsal view to avoid potential errors arising from repositioning the specimens during data collection. Juveniles were excluded due to ontogenetic difference in their skeletal morphology (Young 2006). Specimens showing disease, which deformed the scapulae, or significant amounts of post-mortem damage obscuring collection of three or more landmarks, were also excluded from the analyses. Only one scapula, either left or right, was sampled from each specimen. Most of the specimens measured were from the wild but the *Pygathrix* sample included both wild and captive individuals.

Table 8. Landmarks used following the methods of Young (2006; 2008) and Bailey and Pampush (2015).

	Landmarks
1	Inferior most point of the suprascapular notch
2	Superior most point of the superior angle
3	Central most point of vertebral border and scapular spine intersection
4	Inferior most point of inferior angle
5	Superlatero corner of the teres major attachment site
6	Maximum curvature of the infraglenoid tubercle
7	Maximum curvature of the spinoglenoid notch
8	Medial extent of trapezius attachment on scapular spine
9	Most inferior extent of glenoid fossa
10	Most lateral extent of glenoid fossa
11	Most medial extent of glenoid fossa
12	Most superior extent of glenoid fossa
13	Central maximum curvature of glenoid fossa
14	Medial most portion of the coracoid prominence
15	Superior-lateral tip of the coracoid process
16	Inferior-lateral tip of the coracoid process
17	Distal-most point of the acromion process.

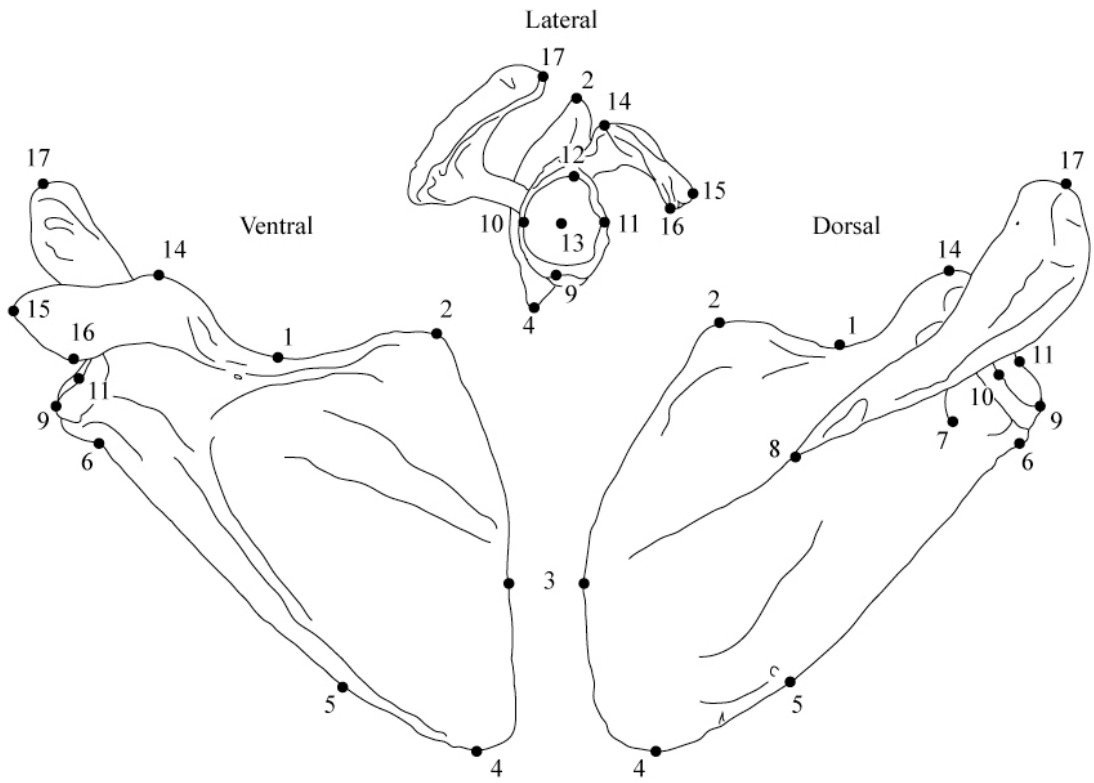


Figure 4. Locations of scapula landmarks measured following the methods of Young (2006; 2008). Figure from Bailey and Pampush (2015).

Table 9. Specimens used in this study. These specimens were sampled opportunistically.

Taxa	Common Name	N	Locomotor Classification (Fleagle 2013; Napier and Napier 1967)	Location and number of specimens collected at each location
<i>Pygathrix cinerea</i>	Grey-shanked douc	14	Unknown	Kon Ka Kinh Primate Conservation Program = 2 Endangered Primate Rescue Center = 12
<i>Pygathrix nemaeus</i>	Red-shanked douc	18	Unknown	Muséum National d'Histoire Naturelle = 2 Endangered Primate Rescue Center = 16
<i>Pygathrix nigripes</i>	Black-shanked douc	3	Unknown	Dalat Museum = 1 Southern Institute of Ecology = 2

Table 9 Continued

Taxa	Common Name	N	Locomotor Classification (Fleagle 2013; Napier and Napier 1967)	Location and number of specimens collected at each location
<i>Ptilocolobus badius</i>	Western red colobus	35	Quadruped	WS McGraw Primate Skeletal Collection, Ohio State University = 35
<i>Cercopithecus diana</i>	Diana monkey	6	Quadruped	WS McGraw Primate Skeletal Collection, Ohio State University = 6
<i>Cercopithecus cambelli</i>	Campbell's monkey	3	Quadruped	WS McGraw Primate Skeletal Collection, Ohio State University = 3
<i>Cercopithecus petaurista</i>	Lesser spot-nosed guenon	3	Quadruped	WS McGraw Primate Skeletal Collection, Ohio State University = 3

Table 9 Continued

Taxa	Common Name	N	Locomotor Classification (Fleagle 2013; Napier and Napier 1967)	Location and number of specimens collected at each location
<i>Trachypithecus germainii</i>	Indochinese lutung	1	Quadruped	Southern Institute of Ecology = 1
<i>Hylobates spp.</i>	Gibbon	4	Brachiator	Muséum National d'Histoire Naturelle = 4
<i>Hylobates lar</i>	White-handed gibbon	2	Brachiator	Muséum National d'Histoire Naturelle = 2
<i>Hylobates moloch</i>	Silvery gibbon	1	Brachiator	Muséum National d'Histoire Naturelle = 1
<i>Hylobates pileatus</i>	Pileated gibbon	1	Brachiator	Muséum National d'Histoire Naturelle = 1
<i>Nomascus gabriellae</i>	Yellow-cheeked gibbon	1	Brachiator	Muséum National d'Histoire Naturelle = 1
<i>Nomascus concolor</i>	Black-crested gibbon	1	Brachiator	Muséum National d'Histoire Naturelle = 1

Table 9 Continued

Taxa	Common Name	N	Locomotor Classification (Fleagle 2013; Napier and Napier 1967)	Location and number of specimens collected at each location
<i>Nomascus leucogenys</i>	Northern white-cheeked gibbon	7	Brachiator	Muséum National d'Histoire Naturelle = 7

For the purposes of this study the three douc langur species, *Pygathrix nemaeus*, *Pygathrix nigripes*, and *Pygathrix cinerea*, were grouped into a single entry (*Pygathrix*) and assigned to the ‘unknown’ locomotor category. This reflects our agnostic position regarding their status as brachiators or quadrupeds. Previous work has found no significant difference in scapular shape between the three species of douc langurs, or between wild and captive specimens (Bailey and Pampush 2015), suggesting their condensation into a single group is appropriate for these analyses. The other cercopithecoids in the sample include *Ptilocolobus badius*, *Cercopithecus diana*, *Cercopithecus campbelli*, *Cercopithecus petaurista*, and *Trachypithecus germainii*. These taxa were assigned to the ‘quadrupedal’ locomotor category, consistent with previous research (e.g. Fleagle 2013; Napier and Napier 1967). The hylobatids (*Hylobates* spp. and *Nomascus* spp.) were

assigned to the ‘brachiator’ locomotor category also based on the literature (e.g. Fleagle 2013; Napier and Napier 1967).

All analyses were completed using the R package geomorph (Adams et al. 2004; R Core Team 2013). The sample includes specimens from both the left and right sides, therefore mirroring was required. A Procrustes analysis was used to uniformly scale and align the point clouds, which allowed for sexes to be pooled together (as scapular size is accounted for with the Procrustes transform). Seven specimens (two *P. nigripes* specimens and five *P. badius* specimens) missing three or fewer landmarks were imputed (i.e., the missing landmarks were statistically reconstructed based on species averages and the other landmarks of the particular individual). A Principal Component Analysis was performed to examine variance in scapular shape and Procrustes ANOVAs were conducted to test for shape differences among the scapulae. A pairwise analysis was conducted to compare the means for the three locomotor groups to determine which groups (if any) were significantly different from each other. To be sure phylogeny was not having an outsized effect on the measure of scapular shape, a phylogenetically controlled Procrustes ANOVA was performed. Performing such an analysis required two additional sets of data. First, a phylogenetic tree was downloaded from 10kTrees (Arnold et al. 2010). Second, a set of mean coordinates was produced for each taxon, this was done using the ‘mean shape’ tool contained within geomorph.

3.3. Results

The three locomotor classifications grouped into distinct morphological clusters in the Principal Component Analysis (Figure 5). Results of the PCA are presented in Table

10 and Figure 5. The wireframes in Figure 5 illustrate the scapula shape of each of the three locomotor categories. The quadrupeds (other cercopithecids) clustered negatively on the first axis and distributed positively and negatively across the second axis (but mainly positively). The brachiators (hylobatids) are clustered positively on the first axis and are predominantly positive on the second axis. *Pygathrix* falls between the cercopithecids and the hylobatids with a positive-negative spread on the first axis and a largely negative distribution across the second axis. PC1 accounts for 39.66% of the observed variation and PC2 accounts for 20.12% of the variation (59.78% cumulatively). PC1 discriminates all three locomotor groups with the greatest variation while PC2 contains more overlap. Positive PC1 scores are characterized by a more inferiorly placed scapular spine along the vertebral border, a relatively longer acromion process (and by extension, scapular spine), and a superiorly oriented glenoid fossa. *Pygathrix* shares a superiorly placed scapular spine along the vertebral border with the cercopithecids and a long acromion process and scapular spine with the hylobatids. The more acute angle between the coracoid prominence and the superior and inferior tips of coracoid process also links *Pygathrix* to other cercopithecids on PC1. This angle on the hylobatids is not nearly as acute. While *Pygathrix* is more similar to the cercopithecids on PC1, they are separated on PC2. Negative PC2 scores are characterized by a more medially placed superior angle thereby shortening the superior border and lengthening the superior aspect of the vertebral border. Additionally, the lower PC2 scores are distinguished by a mediolaterally compressed and craniocaudally elongated scapular body.

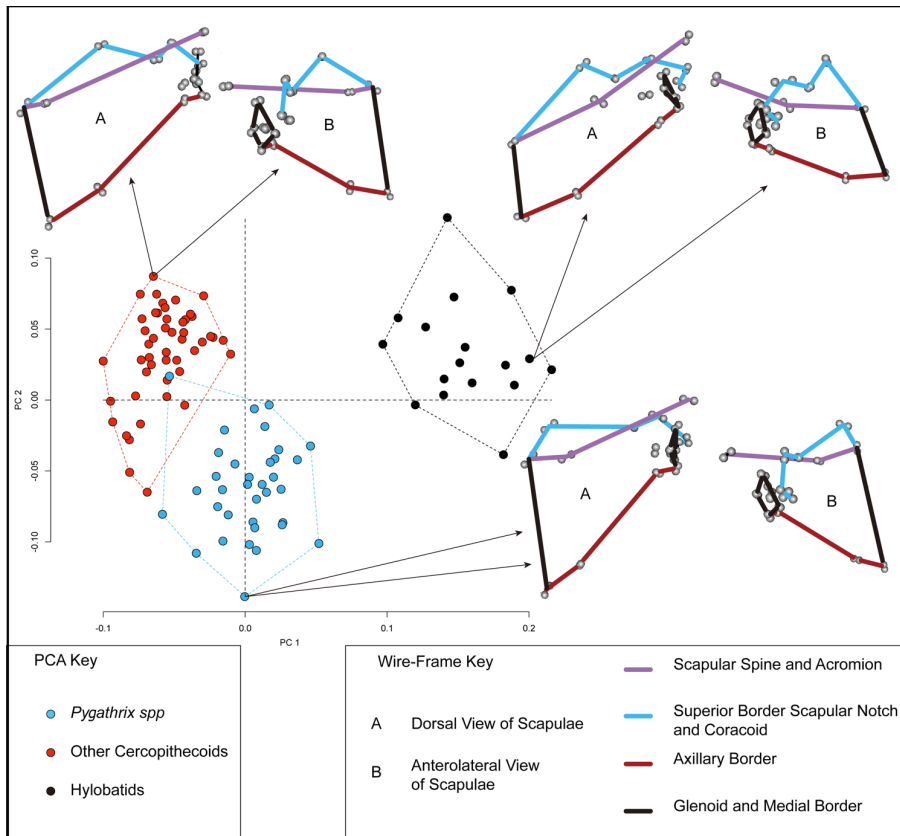


Figure 5. Principal Components Analysis and wireframes of scapula shape. Quadrupeds fall negatively on PC1 and have a positive – negative spread across PC2. *Pygathrix* has a positive – negative distribution across PC1 and a primarily negative distribution across PC1 and a primarily negative distribution across PC2. Brachiatoids are primarily clustering positively on PC1 and mostly positive on PC2.

Wireframes represent the respective scapular shape for each of the three locomotor categories.

Table 10. PCA results.

	PC1	PC2	PC3	PC4	PC5
SD	0.07954	0.05666	0.04191	0.02692	0.02296
Proportion of Variance	0.3966	0.20123	0.11012	0.04544	0.03304
Cumulative Proportion	0.3966	0.59784	0.70796	0.7534	0.78644

An ANOVA comparing scapula shape for all locomotor types indicated significant differences among the groups ($P < 0.01$) (Table 11). Further, pairwise analysis showed *Pygathrix* scapular morphology to be significantly different from both quadrupeds ($P < 0.01$) as well as brachiators ($P < 0.01$) (Tables 12, 13). Results of the phylogenetically controlled Procrustes ANOVA also showed a significant difference ($P = 0.008$) (Table 14).

Table 11. ANOVA Comparing Scapular Shape for All Locomotor Patterns.

	df	SS	MS	η^2	F	P Value
Locomotion	2	0.79749	0.39874	0.50497	49.475	<0.001
Residuals	97	0.78177	0.00806			
Total	99	1.57926	0.01595			

Table 12. Pairwise Analysis Comparing Distance Between Quadrupeds and *Pygathrix*.

	df	SS	MS	η^2	F	P Value
Locomotion	2	0.27007	0.135033	0.30866	17.859	<0.001
Residuals	80	0.60490	0.007561			
Total	82	0.87496	0.010670			

Table 13. Pairwise Analysis Comparing Distance Between Brachiators and *Pygathrix*.

	df	SS	MS	η^2	F	P Value
Locomotion	2	0.38798	0.193989	0.48313	22.9	<0.001
Residuals	49	0.41508	0.008471			
Total	51	0.80306	0.015746			

Table 14. Phylogenetically controlled Procrustes ANOVA.

	df	SS	MS	η^2	Z	P Value
Locomotion	2	0.0017	0.0008	0.001	3.665	0.008
Residuals	12	1.7132	0.1428			
Total	14	1.7159				

3.4. Discussion

The results presented here show that the scapular morphology of *Pygathrix* is distinct from that of both quadrupedal cercopithecids and brachiating hylobatids. The morphology of the douc langur scapula is intermediate between typical brachiators and quadrupeds and may indicate the distinct locomotor repertoire of this genus. On PC1

Pygathrix is similar to other cercopithecids with its long vertebral border but the laterally projecting acromion process, long scapular spine, and more cranially oriented glenoid fossa resemble the hylobatids. On PC2 *Pygathrix* is distinct from both the other cercopithecids and the hylobatids with its mediolaterally compressed scapula and more medially located superior angle.

The difference in η^2 values between the phylogenetically controlled and non-phylogenetically controlled procrustes ANOVAs prompted an unplanned test for phylogenetic signal. This was performed in geomorph using the function ‘physignal’. This returned a Blomberg’s K value of 0.0073 (Table 15), which is very small yet significantly different from zero. So, while there is some effect of shared descent on the distribution of these data, the effect is rather small and is unlikely to be the cause of the η^2 differences. Rather, the difference in η^2 values is likely the product of digesting the point cloud data into species means to perform the phylogenetically corrected analysis. This data aggregation dramatically lowered the number of data points and limited the power of the analysis.

Table 15. Results of the assessment of phylogenetic signal.

Blomberg’s K	p-value	Permutations
0.0073	0.02	1000

Upon casual observation, the *Pygathrix* scapulae resembles that of *Ptilocolobus badius* (Figure 6). However, upon closer inspection there are several characteristics that set them apart. The acromion process is more robust and projects further laterally in *Pygathrix* than the other cercopithecids, in addition to a more robust scapular spine. The relationship of the acromioclavicular joint to arm elevation is an obvious explanation for the more robust acromion found in brachiators (Hunt 1991). A major difference between the hylobatids and the colobines is the teres major attachment site (the boney portion between the teres major fossa and inferior angle). In the colobines, the teres major attachment site projects further laterally compared to the hylobatids (personal observation). In *P. badius*, this has been proposed to be a result of adduction of the forelimb after superior retrieval of food during foraging (Dunham et al. 2016). *Pygathrix* has a teres major attachment site that is similar to *P. badius* but it appears to be not quite as large. The superior angle of the superior border is distributed more medially in the douc langurs compared to both the hylobatids and cercopithecids. A plausible explanation for this is the abundant use of the supraspinatus muscle, which attaches along the superior aspect of the supraspinatus fossa (superior border). The supraspinatus is critical for stabilization in the glenohumeral joint in both brachiators and quadrupeds, and for the elevation of the arm in brachiators (Potau et al. 2011). The glenoid fossa is less cranially oriented in *Pygathrix* than in the hylobatids. These differences are to be expected given how muscle insertions and skeletal morphology of the shoulder girdle of arm-swinging

colobines are described as intermediate between quadrupeds and true brachiators (Ashton and Oxnard 1964a).



Figure 6. Scapula of *Pilocolobus badius* (left), *Pygathrix nemaeus* (center), *Nomascus leucogenys* (right). These three species are the largest representative of their respective locomotor groups in terms of sample size.

Another factor related to below-branch locomotion is body size. A general trend observed within and between primate clades is that as body size increases, the frequency of below-branch locomotion also increases, presumably because it is easier for large-bodied primates to hang below a branch than to balance on top of it (Cartmill 1985a; Fleagle and Mittermeier 1980b; Napier 1967b; Napier and Napier 1967; Ward 2007).

Among the colobines, *Pygathrix* lies towards the larger end of the body mass spectrum (Delson et al. 2000; Smith and Jungers 1997). Colobines that rarely engage in arm-swinging, such as *P. badius* and *Trachypithecus francoisi*, (McGraw 1998a; Zhou et al. 2013) weigh less than the more suspensory *Pygathrix nemaeus*. A parallel trend appears in New World monkeys as well (Fleagle and Mittermeier 1980b). Two groups of large-bodied New World monkeys *Ateles spp.* (spider monkey) and *Lagothrix spp.* (woolly monkey) are well known for their suspensory behaviors (Napier and Napier 1967; Smith and Jungers 1997), with suspensory locomotion comprising 23.3% and 11.7% of travel time, respectively (Cant 1986; DeFler 2000). However, having a larger body size does not necessarily imply an increased use of suspensory behaviors. For example, *Alouatta spp.* infrequently uses suspensory behaviors and weighs between 6 - 7 kg. (with the exception of the *Alouatta pigra* at 11.4 kg.) which is comparable to *Ateles spp.* (between 7 – 9.6 kg) (Fleagle 2013). Smaller New world monkeys, such as *Saimiri boliviensis* use suspensory postures <1% of the time (Arms et al. 2002). The brachiation frequencies of *Ateles* and *Lagothrix* are less than the arm-swinging frequencies reported for *Pygathrix*. Furthermore, another Vietnamese odd-nosed monkey, *Rhinopithecus avunculus* (the Tonkin snub-nosed monkey), arm-swings 5.23% of the time (Le Khac Quyet 2014) and weighs in around 16 kg. (males) (Rowe and Myers 2016). *Semnopithecus entellus* is a species of langur from Asia that are also heavier (~ 16 – 19 kg.) a virtually never use brachiation or arm-swinging behaviors (Rowe and Myers 2016).

The suspensory locomotion used by the atelines differs from that of Old World brachiators by use of a prehensile tail in the former. Use of the prehensile tail results in a

more pronograde suspension in the *Atelines*, compared to the more orthograde suspension observed in *Pygathrix* and the hylobatids (Hunt et al. 1996b). Despite this difference, the scapular morphology of *Ateles* and *Lagothrix* resembles that of the hylobatids (Kagaya 2007); *Ateles* has a wide glenoid fossa while both *Ateles* and *Lagothrix* have a wide supraspinatus fossa (Campbell 1937), which is consistent with typical brachiator morphology (Ashton and Oxnard 1963). Overall, the scapula morphology of *Lagothrix* is described as intermediate between that of *Ateles* and *Alouatta*, with *Ateles* being the most similar to the hylobatids and *Alouatta* representing a more typical quadruped (Gebo 1996). Further, both *Ateles* and *Lagothrix* have a cranially oriented glenoid fossa (Gebo 1996) a feature they share with *Pygathrix* and the hylobatids. Features shared by these taxa may be helpful for identifying suspensory behaviors in the fossil record. If such features appear in concordance with body size increases during hominoid evolution, particularly in the hylobatid evolution, this could be a useful line of evidence illuminating the below-branch locomotion in this clade.

This study lays the foundation for future research. A wild-based study focusing exclusively on locomotion and positional behaviors is the next logical step in identifying factors influencing arm-swinging frequency in douc langurs' natural habitat. Coupled with the present scapular morphology investigation, a locomotor study could explain why arm-swinging is observed in this genus at frequencies unique among colobines. It would be beneficial to incorporate more odd-nosed taxa into morphological studies to draw comparisons to the douc langurs. Furthermore, red and black-shanked douc langurs are classified as Endangered and grey-shanked douc langurs are classified as Critically

Endangered by the International Union for Conservation of Nature (IUCN) (Rawson et al. 2008; Vu Ngoc Thanh et al. 2008a; Vu Ngoc Thanh et al. 2008b). Behavioral and ecological data are imperative for ensuring their future conservation.

CHAPTER IV
THE RELATIONSHIP BETWEEN THE GLENOID FOSSA AND THE ACRIOMION
PROCESS IN PRIMATES

4.1. Introduction

Generally primates are classified into four broad locomotor categories: quadrupeds, brachiators, leapers, and bipeds (Napier and Napier 1985). Although behavioral locomotor designations can be imprecise, these locomotor categories offer a structure for developing and organizing future research (Napier and Napier 1967). Quadrupeds and brachiators rely more heavily on their forelimb for locomotion (in contrast to leapers and bipeds which rely more on the hindlimb) (Ashton and Oxnard 1964b). Each of these broad designations have subcategories to acknowledge that primates move in a variety of ways. For example, *Pygathrix spp.* were historically placed under the broad quadrupedal category (Napier and Napier 1985; Napier and Napier 1967) but are known to exhibit high proportions of arm-swinging behavior in captivity (Byron and Covert 2004; Hollihn 1973; Wright et al. 2008), in addition to quadrupedalism and leaping.

Anatomical studies of the primate forelimb are frequently used to explain locomotor behavior in both extinct and extant primates (e.g. Ashton and Oxnard 1964a; Dunham et al. 2016; Green and Alemseged 2012). The scapula has a suite of traits that together can generally predict an animal's locomotor capabilities. For example, suspensory/brachiating primates have a more dorsally placed scapula (Gebo 1996) and a

more cranially oriented glenoid fossa (Larson 1993). Conversely, quadrupedal primates have a more laterally placed and wider scapula (across the scapular spine) (Larson 1993). Bipedal primates have a dorsally placed scapula and a laterally oriented glenoid fossa (Figure 7) (Ashton and Oxnard 1964a). In addition to the scapula, the clavicle is known to be longer in suspensory primates and shorter in primates that do not exhibit high proportions of overhead-arm behavior (Ashton and Oxnard 1964a; Jenkins et al. 1978). This lengthening is particularly evident in brachiators because the traditional thoracic shape of hominoids is ‘flattened’ dorsoventrally (Chan 1997; Kagaya et al. 2008), which places their scapula further dorsally and thereby elongates both the clavicle and acromion process to allow them meet along the coronal plane (Jenkins et al. 1978; Voisin 2006).



Figure 7. Scapula representations of the four locomotor categories. L-R *Ptilocolobus badius*, *Pygathrix cinerea*, *Nomascus leucogenys*, and *Homo sapiens*. Figure adapted from Bailey and Pampush (2015).

The acromion process is recognized to be more robust in the hominoids, which is correlated with a more robust deltoid muscle (Ciochon and Corruccini 1977). The deltoid muscle originates on the acromion process and the clavicle and works to stabilize the glenohumeral joint, which is especially important in a brachiating anatomy such as seen in gibbons (Ashton et al. 1965; Jungers and Stern 1981). The lateral projection of the coracoid and acromion processes and the shape of the glenoid fossa have been noted to discriminate the hominoids from other anthropoids because only the hominoids have a coraco-acromial ligament (Ciochon and Corruccini 1977). Additionally, the trapezius muscle also attaches on the acromion process and assists to rotate the scapula on the thoracic wall (Moore et al. 2002). Given the origins and attachments of the aforementioned muscles, I speculate that the acromion process of brachiators is likely more robust than in primates that do not require extensive overhead arm-use.

The goal of this article is to determine if locomotor patterns in primates are identifiable based on specific limited morphological features. Previously, most studies have focused on general scapular shape (e.g. Melillo 2016; Oxnard 1969; Young 2008), the bar-glenoid angle (e.g. Green and Alemseged 2012; Stern and Susman 1983) or scapular indices (e.g. Ashton et al. 1965; Covert et al. 2004; Su and Jablonski 2008) as a reflection of locomotor capabilities. Given the central role the acromion process plays in arm-use, we attempt here to discern locomotor designations, particularly in forelimb

dependent primates, based on the straight-line distance the acromion process projects past the glenoid fossa. Based on previously reported proportions of overhead-arm use, I expect brachiators to have the greatest acromion process projection, followed by arm-swingers, quadrupeds, then bipeds. Gibbons use brachiation approximately 74 - 80% of the time during travel (Andrews and Groves 1976; Gittins 1983), captive douc langurs use arm-swinging approximately 50% of the time during travel (Byron and Covert 2004; Wright et al. 2008), and the western red colobus (*Ptilocolobus badius*—the largest representative of cercopithecids in this study) only arm-swing 2.9% and use quadrupedal behaviors 54.8% of the time during travel (McGraw 1998b).

4.1.1. Methods

We assigned the locomotor categories for all specimens based on existing literature. The representative quadrupeds include *Ptilocolobus badius* (McGraw 1998b), *Cercopithecus diana* (McGraw 1998b), *Cercopithecus campbelli* (McGraw 1998b), *Cercopithecus petaurista* (Fleagle 2013), and *Trachypithecus germainii* (Fleagle 2013). The brachiators are represented by *Hylobates spp.*, *Hylobates lar*, *Hylobates moloch*, *Hylobates pileatus*, *Nomascus gabriellae*, *Nomascus concolor*, and *Nomascus leucogenys* (Fleagle 2013). *Pygathrix spp.* was included in a separate category (arm swingers), given more recent studies demonstrating their arm-swinging behavior in captivity (Byron and Covert 2004; Wright et al. 2008) and given that their scapula is significantly different in shape from both quadrupeds and brachiators (Bailey et al. 2017). All three species of *Pygathrix* are able to be pooled together because their scapula are not significantly

different in shape (Bailey and Pampush 2015). In this study, bipeds are represented by *Homo sapiens*.

Using a Microscribe (Immersion Technologies, San Jose, CA.), 17 landmarks (Figure 8) (Young 2006, 2008) were collected on the scapula of: brachiators (n = 18), quadrupeds (n = 48), arm-swingers (*Pygathrix*) (n = 35), and bipeds (n = 13). All scapulae were sampled from adult specimens from museum, rescue center, university, and conservation agency collections (Table 16). All landmarks were recorded from the dorsal view to avoid observer error. Landmark data is ideal for this particular study because through the analysis, size differences related to sex are controlled by a Generalized Procrustes Analysis (Zelditch et al. 2012). The landmark data was imported via a Microsoft Excel file and analyzed in the R package geomorph (Adams and Otárola-Castillo 2013). Specimens were chosen on the requirement of having at least 15 landmarks present (i.e. not broken or fragmented in more than two places). Missing landmarks were estimated and imputed for seven specimens (two arm-swingers, five quadrupeds). Imputation estimates where missing landmarks from the incomplete specimen would be based on a reference point from a complete specimen. A Procrustes Analysis was used to uniformly scale the data to control for sex and side and place the scapulae into the same morphospace. Landmarks 13 (the center-most point of the glenoid fossa) and 17 (the distal-most tip of the acromion process) were then isolated and the straight-line distance between these two points was calculated for all individuals. None of the chosen specimens were missing landmarks 13 and 17 and therefore imputation was not required for the critical landmarks. An analysis of variance (ANOVA) was performed to test if there was

a difference between all four locomotor categories, the broad locomotor categories (bipeds, brachiators, and quadrupeds), and the forelimb dependent locomotor categories (brachiators, quadrupeds, and arm-swingers). A Tukey's Honest Significant Difference (HSD) test was used to test if the means were significantly different from one another, first with all four locomotor categories, second with the three broad locomotor categories, and third with the forelimb dependent primates. The benefit of using a Tukey's HSD test is that it automatically adjusts the p-value for multiple comparisons.

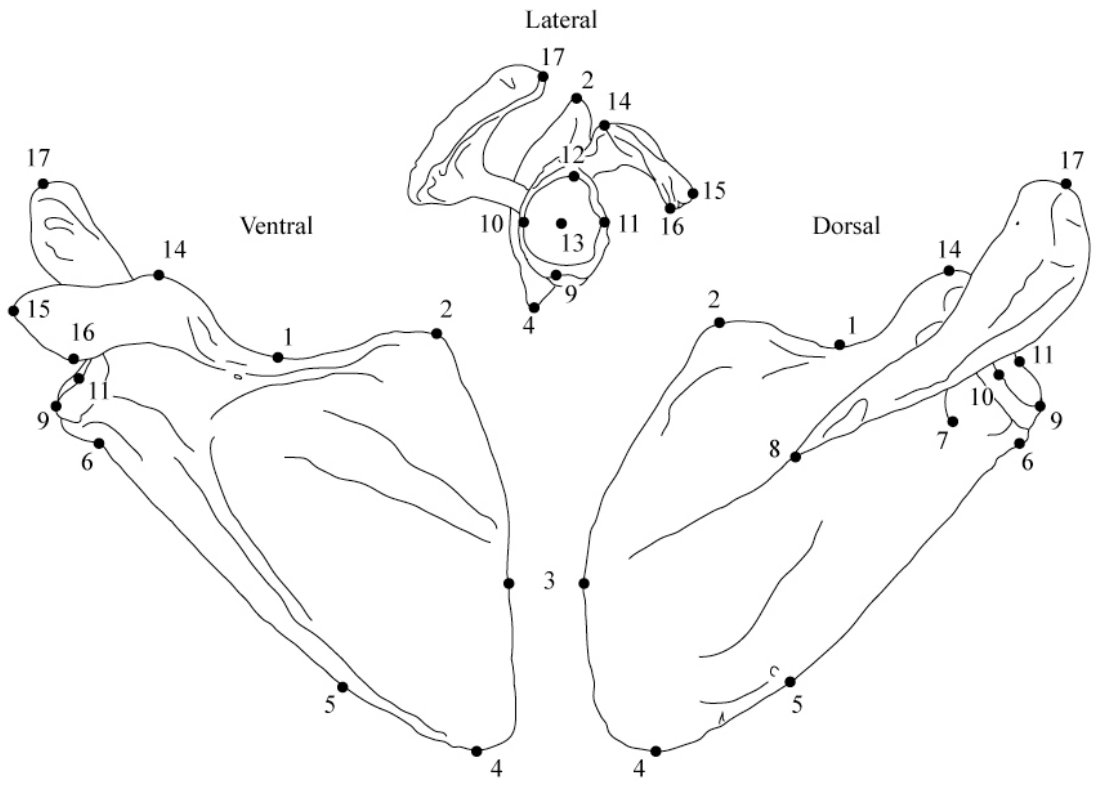


Figure 8. Landmarks used. Figure from Bailey and Pampush (2015).

Table 16. Specimens used in this study were sampled opportunistically. Table reprinted from Bailey and Pampush (2015).

Taxa	Common Name	N	Locomotor Classification (Fleagle 2013; Napier and Napier 1967)	Location and number of specimens collected at each location
<i>Pygathrix cinerea</i>	Grey-shanked douc	14	Unknown	Kon Ka Kinh Primate Conservation Program = 2 Endangered Primate Rescue Center = 12
<i>Pygathrix nemaeus</i>	Red-shanked douc	18	Unknown	Muséum National d'Histoire Naturelle = 2 Endangered Primate Rescue Center = 16
<i>Pygathrix nigripes</i>	Black-shanked douc	3	Unknown	Dalat Museum = 1 Southern Institute of Ecology = 2

Table 16 Continued

Taxa	Common Name	N	Locomotor Classification (Fleagle 2013; Napier and Napier 1967)	Location and number of specimens collected at each location
<i>Ptilocolobus badius</i>	Western red colobus	35	Quadruped	WS McGraw Primate Skeletal Collection, Ohio State University = 35
<i>Cercopithecus diana</i>	Diana monkey	6	Quadruped	WS McGraw Primate Skeletal Collection, Ohio State University = 6
<i>Cercopithecus cambelli</i>	Campbell's monkey	3	Quadruped	WS McGraw Primate Skeletal Collection, Ohio State University = 3
<i>Cercopithecus petaurista</i>	Lesser spot-nosed guenon	3	Quadruped	WS McGraw Primate Skeletal Collection, Ohio State University = 3

Table 16 Continued

Taxa	Common Name	N	Locomotor Classification (Fleagle 2013; Napier and Napier 1967)	Location and number of specimens collected at each location
<i>Trachypithecus germainii</i>	Indochinese lutung	1	Quadruped	Southern Institute of Ecology = 1
<i>Hylobates spp.</i>	Gibbon	4	Brachiator	Muséum National d'Histoire Naturelle = 4
<i>Hylobates lar</i>	White-handed gibbon	2	Brachiator	Muséum National d'Histoire Naturelle = 2
<i>Hylobates moloch</i>	Silvery gibbon	1	Brachiator	Muséum National d'Histoire Naturelle = 1
<i>Hylobates pileatus</i>	Pileated gibbon	1	Brachiator	Muséum National d'Histoire Naturelle = 1
<i>Nomascus gabriellae</i>	Yellow-cheeked gibbon	1	Brachiator	Muséum National d'Histoire Naturelle = 1
<i>Nomascus concolor</i>	Black-crested gibbon	1	Brachiator	Muséum National d'Histoire Naturelle = 1

Table 16 Continued

Taxa	Common Name	N	Locomotor Classification (Fleagle 2013; Napier and Napier 1967)	Location and number of specimens collected at each location
<i>Nomascus leucogenys</i>	Northern white-cheeked gibbon	7	Brachiator	Muséum National d'Histoire Naturelle = 7
<i>Homo sapiens</i>	Humans	13	Biped	Department of Anthropology Teaching Collection, Texas A&M University

4.2. Results

There was a significant effect of locomotor category on the relative distance between the glenoid fossa and the acromion process (ANOVA: $\alpha=0.05$, $F(3, 111)=72.87$, $p<0.01$) (Table 17). This effect still remains after excluding bipeds to compare forelimb dependent locomotor categories ($F(2,98)=59.17$, $p<0.01$). This effect also remains after excluding the arm-swinger category in order to focus on broader categories ($F(2,77)=76.05$, $p<0.01$). A post-hoc Tukey's showed a significant difference between brachiators and bipeds ($p<0.01$), quadrupeds and bipeds ($p<0.01$), arm-swingers and bipeds ($p<0.01$), and quadrupeds and bipeds ($p=0.03$) (Table 18, Figure 9). There is no significant difference between arm-swingers and brachiators ($p=0.85$) or arm-swingers and quadrupeds ($p=0.08$) (Table 18). When comparing the broad locomotor categories (bipeds, brachiators, and quadrupeds), the ANOVA shows a significant difference ($p<0.01$) (Table 19, Figure 10). The result of the Tukey's HSD shows a significant difference between brachiators and bipeds ($p<0.01$), quadrupeds and bipeds ($p<0.01$), and the difference between quadrupeds and brachiators is approaching significance ($p=0.06$) (Table 20). Next, when comparing the forelimb dependent primates (i.e. primates that are required to use the forelimb for locomotion), the ANOVA shows a significant difference ($p<0.01$) (Table 21, Figure 11). The Tukey's HSD shows a significant difference between all comparisons (quadrupeds and brachiators, $p<0.01$; arm-swingers and brachiators, $p=0.01$; arm-swingers and quadrupeds $p<0.01$) (Table 22).

Table 17. Results of the ANOVA between all locomotor categories.

	DF	Sum of Squares	Mean Square	F Value	P Value
Locomotion	3	0.4138	0.13792	72.87	p < 0.01
Residuals	111	0.2101	0.00189		

Table 18. Results of Tukey's HSD between all locomotor categories.

Locomotor Category Comparisons	<i>p</i> – value
Brachiators – Bipeds	p < 0.01
Quadrupeds – Bipeds	p < 0.01
Arm-Swingers – Bipeds	p < 0.01
Quadrupeds – Brachiators	p = 0.03
Arm-Swingers – Brachiators	p = 0.85
Arm-Swingers – Quadrupeds	p = 0.08

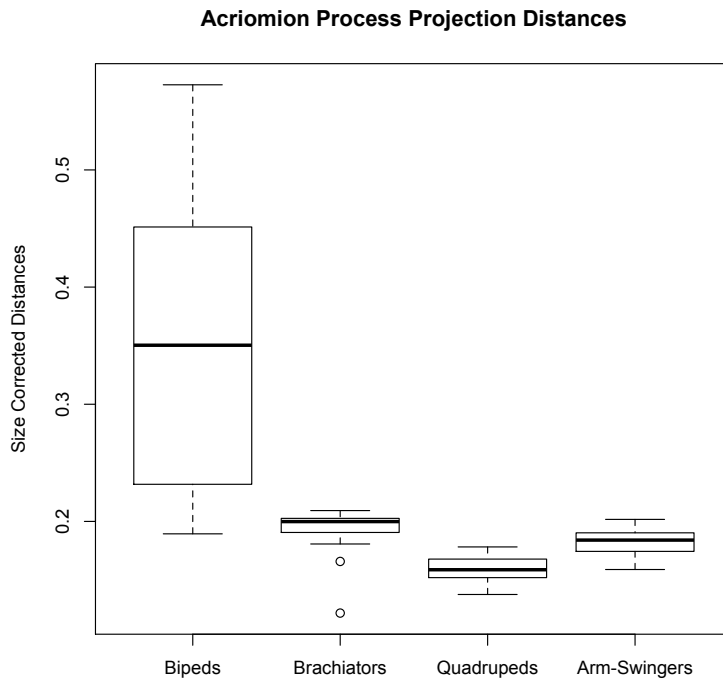


Figure 9. Boxplot of all four locomotor categories.

Table 19. Results of the ANOVA between bipeds, brachiators, and quadrupeds.

	DF	Sum of Squares	Mean Square	F Value	P Value
Locomotion	2	0.4037	0.20187	76.05	$p < 0.01$
Residuals	77	0.2044	0.00265		

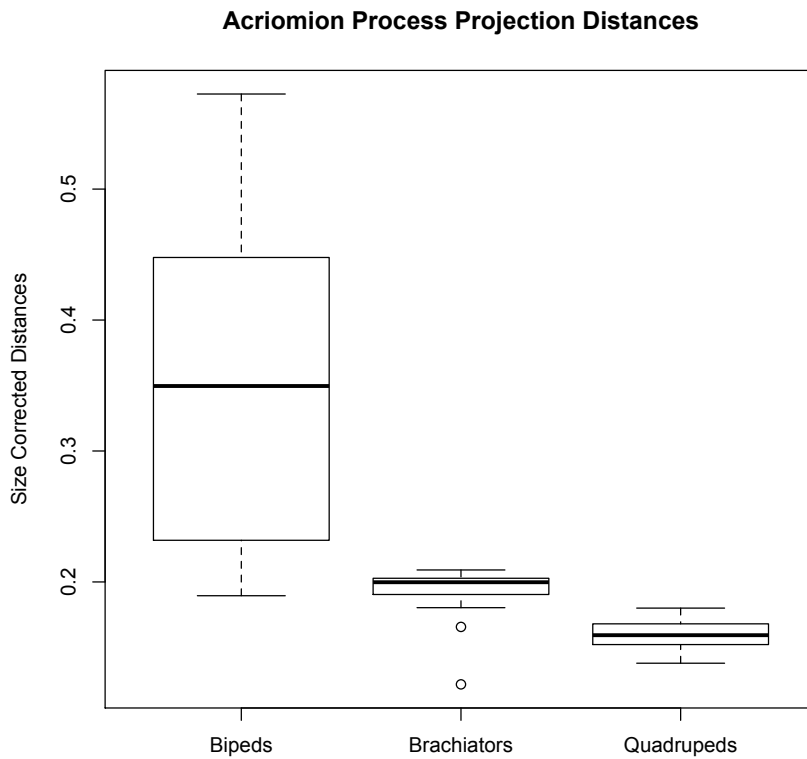


Figure 10. Boxplot of broad locomotor categories excluding arm-swingers (*Pygathrix*).

Table 20. Results of Tukey’s HSD between bipeds, brachiators, and quadrupeds.

Locomotion	p – value
Brachiators – Bipeds	p < 0.01
Quadrupeds – Bipeds	p < 0.01
Quadrupeds – Brachiators	p = 0.06

Table 21. Results of the ANOVA between brachiators, quadrupeds, and arm-swingers.

	DF	Sum of Squares	Mean Square	F Value	P Value
Locomotion	2	0.01896	0.00948	59.17	p < 0.01
Residuals	98	0.01570	0.00016		

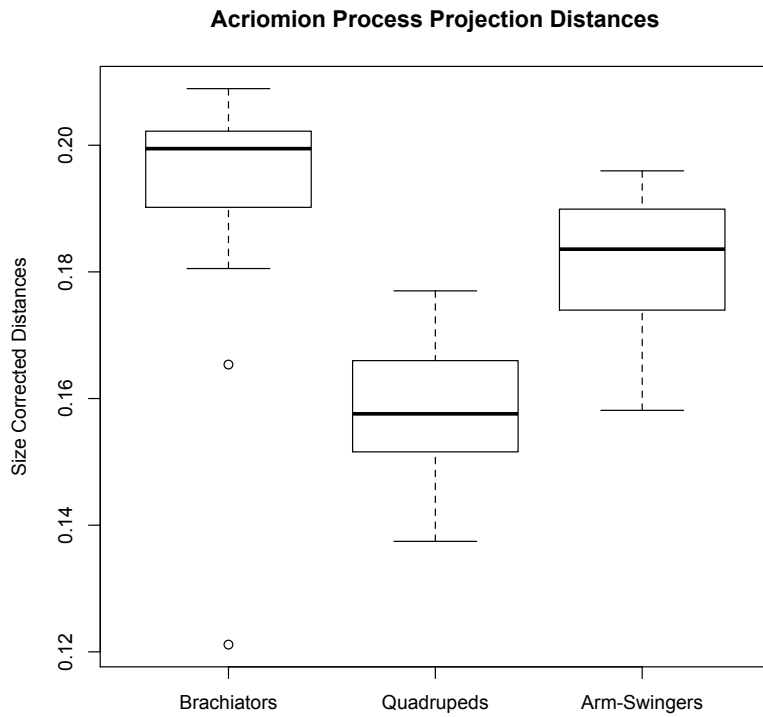


Figure 11. Boxplot of locomotor categories for forelimb dependent primates.

Table 22. Results of Tukey's HSD between brachiators, quadrapeds, and arm-swingers.

Locomotion	p-value
Quadrapeds – Brachiators	p < 0.01
Arm-Swingers – Brachiators	p = 0.01
Arm-Swingers – Quadrapeds	p < 0.01

4.3. Discussion

The results presented here indicate that the distance between the glenoid fossa and acromion process may be used to interpret locomotor categories that rely more predominantly on forelimb use (brachiators, quadrupeds, arm-swingers). More nuanced categories (e.g. arboreal quadruped, terrestrial quadruped, quadrumanual) may not be as reliably interpreted when comparing all locomotor categories. Additionally, despite bipeds not using their arms for locomotor purposes, bipeds had the greatest acromion process projection, even after size correction. Considering this lack of arm use, these results are only biologically significant for those primates that routinely use below-branch locomotion. The range of variation in the distance between the acromion process and the glenoid fossa in bipeds is likely influenced by the fact that locomotion isn't constraining these morphological features.

The acromion process projection differences exhibited among the forelimb dependent primates are reasonably explained by the amount of overhead arm-use these primates employ. For example, *Hylobates* brachiates the most, *Pygathrix* in contrast arm-swings approximately 50% of the time (in captivity) (Byron and Covert 2004; Wright et al. 2008), and *Ptilocolobus badius* only arm-swings 2.9% of the time (McGraw 1998b). These differences predict the robusticity of the acromion process projection for two major reasons. First, the clavicle provides leverage and attachment sites for the muscles of the

shoulder to increase shoulder mobility (Squyres and DeLeon 2015). Second, the deltoid muscle contributes to the efficiency of arm elevation and stabilizes the joint (Ashton et al. 1965). The deltoid overlays the clavicle, acromion process, and humerus (Jungers and Stern 1981; Larson 1993) and is larger and more developed in obligate brachiators (Ashton and Oxnard 1963).

The information in this study may be useful when reconstructing behavior in the primate fossil record and has relevance for understanding the locomotion of past primates, particularly for those that were probably forelimb dependent. For example, the fossil *Australopithecus afarensis* has been the subject of numerous debates in terms of its locomotion. Reconstructing the locomotion of *A. afarensis* is difficult because its scapula shares features with both bipeds and suspensory primates (Stern and Susman 1983). Stern and Susman (1983) specifically identified the cranially oriented glenoid fossa (using the bar-glenoid angle) to be indicative of habitual overhead-arm use. However, a later study incorporated other angles (e.g. axillary-vertebral, glenoid-spinal, bar-glenoid, glenoid-axillary, and spinal-axillary angle) and found *A. afarensis* to group with bipeds (Haile-Selassie et al. 2010). Furthermore, Melillo (2016) described the scapula of *A. afarensis* to be more indicative of bipedalism and that it was unclear if the remaining primitive morphological features enhanced overhead-arm use. By including glenoid-acromion process projection into future primate scapular studies in extinct species, the field may be able to refine current methods for determining locomotor patterns, especially when fossils are frequently fragmented. Future research should include immature scapulae to determine

if ontogenetic differences in locomotor patterns are also discernable from the glenoid-acromion process projection.

CHAPTER V

ARM-SWINGING OF THE RED-SHANKED DOUC LANGUR (*PYGATHRIX NEMAEUS*): IMPLICATIONS OF BODY SIZE

5.1. Introduction

Colobines are well known for being primarily arborealists, with leaping and quadrupedalism being common locomotor behaviors (e.g. Davies and Oates 1994). While below-branch locomotion is routinely observed in the hominoids and the atelines, it was thought to be extremely rare among colobines until it was recently observed in captive douc langurs (genus *Pygathrix*) (Byron and Covert 2004; Fleagle 2013; Napier and Napier 1967). *Pygathrix* consists of three species: *Pygathrix cinerea* (the grey-shanked douc), *Pygathrix nigripes* (the black-shanked douc), and *Pygathrix nemaeus* (the red-shanked douc), and little has been published about the ecological behavior including their positional behavior.

In two studies the red and grey-shanked doucs have been observed using below-branch locomotion (suspensory and arm-swinging) in about 50% of all locomotor bouts in captivity at the Endangered Primate Rescue Center (EPRC) (Byron and Covert 2004; Wright et al. 2008). In another study at the EPRC, adult red-shanked doucs used suspensory locomotion 21.8% of the time and young doucs used suspensory locomotion 25.4% of the time (Workman and Covert 2005). *Pygathrix* was first observed arm-swinging in zoos (Hollihn 1973) prior to the research conducted at the EPRC (Byron and Covert 2004; Workman and Covert 2005; Wright et al. 2008). The EPRC houses

numerous colobines (including non-*Pygathrix* species) in enclosures that are structurally similar (Byron and Covert 2004; Workman and Covert 2005) thus reducing the likelihood that locomotor differences between *Pygathrix* and other colobines at the EPRC are related to the captive environment. Byron and Covert (2004) observed that *P. nemaeus* employed suspensory locomotion 46% of the time in all locomotor bouts at the EPRC. This proportion is in contrast to two other colobines, Delacour's langur (*Trachypithecus delacouri*) and the Hatinh langur (*Trachypithecus laotum hatinhensis*) which only used non-suspensory locomotion. Workman and Covert (2005) further expanded the study to include the ontogeny of locomotion of the red-shanked douc, Delacour's langur, and Hatinh langur at the EPRC. They found both adult and young red-shanked douc langurs to exhibit more suspensory locomotion (~ 22%) than the Hatinh langurs (~2%) and the Delacour's langurs (<1%). Wright et al. (2008) examined the suspensory behavior and kinematic profile of the red and grey-shanked doucs to compare to the behavior of the northern white-cheeked gibbon (*Nomascus leucogenys*) at the EPRC. They found that the red-shanked douc uses suspensory locomotion 46% of the time and grey-shanked doucs use suspensory locomotion 56% of the time. Their results showed that kinematically, the doucs are capable of moving in similar ways to the gibbons, although at a much slower pace. Similarly, Granatosky (2015) found the red-shanked douc to have similar kinetic patterns to *Hylobates* (gibbons) (albeit with some slight differences) and described their arm-swinging at the EPRC as a pendulum. Because of these results, we hereafter designate the locomotor behavior of the doucs as arm-swinging to differentiate from the typical brachiation observed in gibbons.

In conjunction with the behavioral observations at the EPRC, there have been five skeletal studies conducted on *Pygathrix* to identify patterns in the relationship between locomotor behavior and morphology. First, Covert et al. (2004) examined the scapular indices of the doucs and found they retain a longer vertebral border compared to other colobines, which is more consistent with hominoid morphology. Additionally, they found the doucs have a high brachial index (radius length/humerus index), also consistent with the hominoids. The odd-nosed monkey clade (of which *Pygathrix* is a member) also shares a similar skeletal shape of the shoulder girdle and forelimb. Second, Su and Jablonski (2008) investigated skeletal components of the odd nosed monkeys and found all four genera share similar scapular indices, relative olecranon length, intermembral index, clavicular length, and humeral length. They also remarked that the scapular indices of the odd-nosed monkeys were similar to that of extant apes and differed from other Old-World monkeys. Third, since the EPRC studies did not include the black-shanked douc, Bailey and Pampush (2015) conducted a study including this species in an attempt to identify if the all douc langurs retain a similar scapular shape. Results showed that there was no significant difference in scapular shape between the three species of *Pygathrix*, thereby providing some evidence that all species likely share similar locomotor patterns. Fourth, Bailey et al. (2017) compared the scapula of the douc langurs to two other groups of primates; quadrupeds (other cercopithecids) and true brachiators (the hylobatids) and found that *Pygathrix* had an intermediary scapular shape between brachiators and quadrupeds. Fifth, Byron et al. (2017) found the doucs to have a brachial index, crural index, and scapular shape to be comparable to gibbons, while the intermembral index was

more intermediate. All of the aforementioned results suggest that *Pygathrix* is exhibiting some arm-swinging behaviors in the wild.

Despite the extensive captive locomotor studies and numerous morphological investigations, there has yet to be a study focusing exclusively on locomotion in the wild for any of the three species of *Pygathrix*. Previous work from the wild has primarily focused on the socioecology, feeding ecology, and activity budgets of the doucs (e.g. Dinh Thi Phuong Anh et al. 2010; Ha Thang Long 2007; Ha Thang Long 2009; Ha Thang Long et al. 2010; Hoang Minh Duc et al. 2009; Phiapalath 2009; Rawson 2009; Ulibarri 2013). Rawson (2009), however, completed a study on the socioecology of the black-shanked douc langur and reported suspensory behavior to comprise 10% of males', and 3.7% of females' locomotor repertoire.

Notwithstanding the anatomical evidence and captive data indicating *Pygathrix* is arm-swinging in the wild, it remains unclear *why* the doucs are arm-swinging when most other colobines do not. Among colobines, *Pygathrix* lies at the larger end of the body size spectrum, but when considering just Presbytini, *Pygathrix* is mid-sized (Figure 12) (Delson et al. 2000; Le Khac Quyet 2014; Smith and Jungers 1997). It has been long established that an increased body size among primates lends itself to below-branch locomotion (e.g. Cant 1992; Cartmill 1985b; Fleagle and Mittermeier 1980a; Napier 1967a; Napier and Napier 1985; Ward 2002). An increased body size facilitates below-branch locomotion (i.e. suspensory, brachiation, arm-swinging) through elongated arms (Cartmill and Milton 1977) and lowering the center of gravity to avoid overbalancing and compensatory movements that are required above the branch (Grand 1972; Napier and

Napier 1985). Wright et al. (2008) suggested that a combination of an increased body size and diet might have selected for suspensory adaptations in doucs and snub-nosed monkeys. In an effort to tease apart this suggestion, we aim to identify if body size is influencing the frequency of brachiation in the red-shanked douc langur in the wild. We speculate that an increased body size could be the primary mechanism influencing this derived locomotor behavior (relative to other colobines) but given that even larger Asian colobines engage in low levels of arm-swinging it is questionable. This conjecture is testable by comparing body sizes via age and sex classes within the species *P. nemaesus*. Given the differences in percentage of suspensory behavior observed between the sexes of the black-shanked doucs (Rawson 2009), we predict males will arm-swing the most, followed by adult females with a baby on their belly, adult females without a baby, subadults of any sex, and infants of any sex, respectively. We specifically aim to find out at what frequency *P. nemaesus* is arm-swinging in the wild, and to what extent is body size influencing these frequencies.

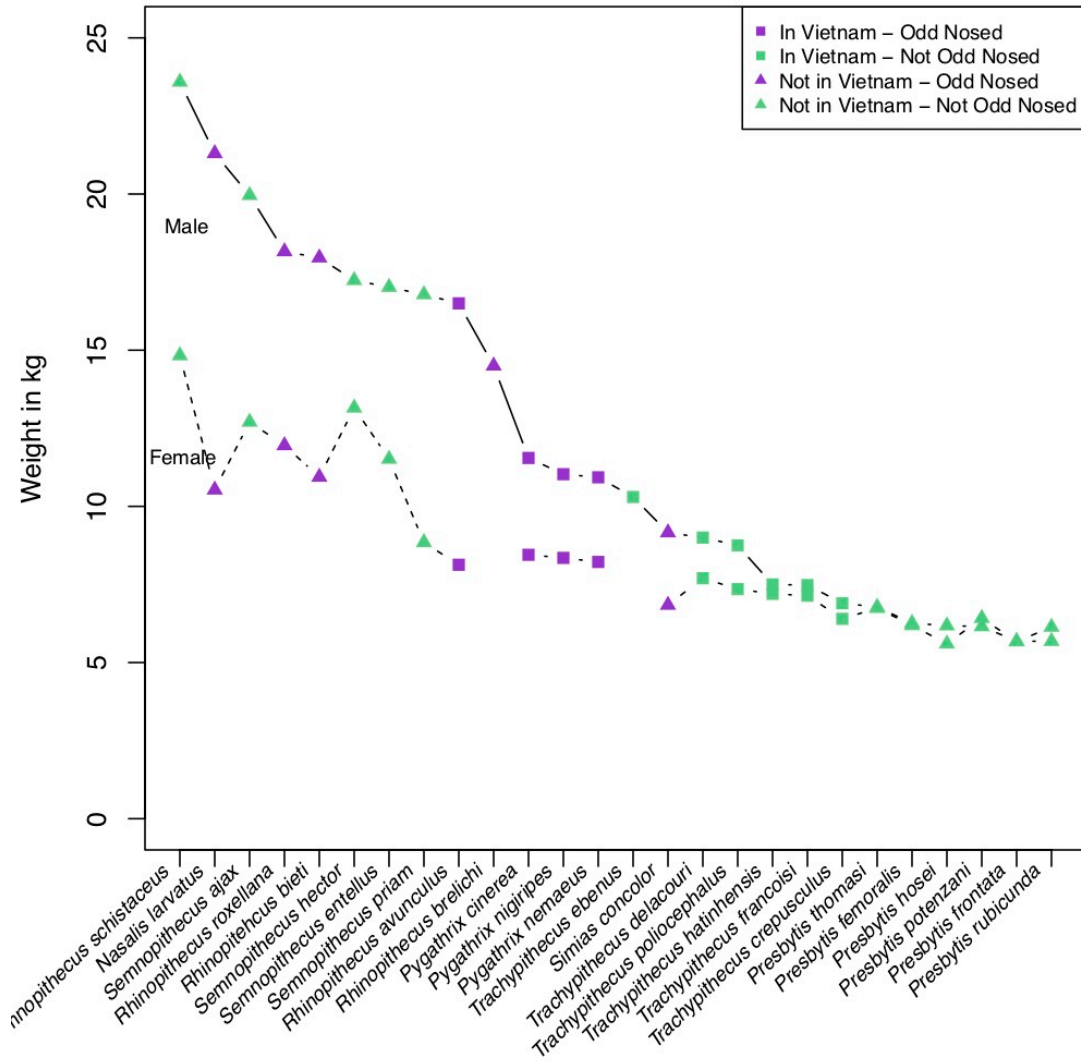


Figure 12. Plot of Presbytini body weights (Delson et al. 2000; Fleagle 2013; Le Khac Quyet 2014; Smith and Jungers 1997).

5.2. Methods

Data were collected in the Son Tra Nature Reserve between November 4th, 2016 and March 13th, 2017 most days, Monday through Friday (approximately 90 contact hours between those dates). The coastal region of Vietnam where Son Tra is located is subject to two primary seasons; the monsoon (wet) season and the dry season (Van Peenen et al. 1971). The November – March timeframe straddled the two seasons thereby ruling out seasonality biases. Son Tra Nature Reserve was established in 1992 initially with 4,439 ha (Sourcebook, 2004) but has since been reduced to 2,670 ha after a portion was reallocated for development (Lippold and Thanh 2008; Sourcebook 2004; Vietnam Conservation Fund 2009). It is adjacent to Da Nang, Vietnam's third largest city.

Throughout the reserve there is a road that circumnavigates the coast and intersects through the middle of the mountain creating fragmented forest patches. The doucs observed in this study were already habituated because Vietnamese photographers come up the mountain almost every day to photograph the monkeys. Because the red-shanked doucs feed on morning glory (*Ipomoea eberhardtii*) that grows extensively along the road, most data was collected from the vantage point of the road. This view also allowed for greater visibility across the forest canopy, which was essential since the doucs were being filmed.

A Canon Vixia handheld camera or a Canon 70D DSLR with a 250mm lens were used to gather footage of the doucs. To maximize the number of observations across the maximum number of individuals, anytime a group or individual moved out of sight or were no longer in visible range, a new group was located and filmed. After completing

data collection in Da Nang, the videos were viewed by one researcher and data were recorded in Excel. Data were continuously recorded for all visible individuals in each video clip for all age and sex classes. The following information was recorded for each bout of behavior: video clip number, individual ID, age, sex, baby on belly, and locomotor behavior (Table 23). Locomotor behaviors were chosen based on broad categories (Hunt et al. 1996a) to offer more comparability between studies. Discrete body size estimates were assigned based on literature from both wild caught and zoo specimens (Table 24) (Delson et al. 2000; Smith and Jungers 1997). Body size was estimated for juveniles by taking the midpoint between average neonate weight and weight at weaning (Lee et al. 1991). Body size was estimated for subadults by taking the midpoint between weight at weaning and average female adult weight (Lee et al. 1991; Smith and Jungers 1997). Body size for adult females with a baby was estimated by adding average adult female body weight to neonate weight (Lee et al. 1991; Smith and Jungers 1997). Age classes were identified following the descriptions of Ulibarri (2013).

It was not possible to learn each individual so a unique ID was assigned to each monkey visible in the clip until the individual moved out of sight or the clip ended. To account for ID as a random effect, a generalized linear mixed model with a logit link function was used to analyze the data in the R packages *tidyr* (Wickham and Henry 2017), *readxl* (Wickham 2015), *lme4* (Bates et al. 2015), and *glmm* (Knudson 2018). All lines of data containing an ‘unknown’ for the following categories were removed from the analysis: baby on belly, age, and sex. These lines of data were removed because the analysis was dependent on knowing those categories. To account for any autocorrelation that might

arise from continuous data collection, two variations of the data were examined as the unit of analysis: first, every locomotor stride and second, only the initial locomotor stride for each locomotor bout (defined as a series of consecutive strides until the locomotion bout stopped). For both types of locomotor data (all strides/initial strides), we conducted the GLMM analyses using both a discrete body-size predictor variable as well as a continuous body-size estimate predictor variable based on the published average masses described above. Using discrete body size estimates considers that weight differences between each of the groups (i.e. adult males, adult females with babies, adult females, subadults, and juveniles). The continuous data analysis acknowledges that the body size lies along a spectrum. Additionally, we calculated the predicted portion of arm-swinging behavior for both datatypes and identified the proportions of locomotor behaviors used for all age and sex classes.

Table 23. Ethogram of locomotor behaviors (Hunt et al. 1996).

Arm-Swing	Hand over hand progression, propelling the trunk forward
Quadrupedal run/walk	Four limb sequence walk/ run across substrate
Leap	Four limbs leave substrate for a period of time while traveling using significant muscle propulsion
Climb	Hand over hand, foot over foot diagonal sequence propulsion, usually going up
Drop	Release from a support by falling down to another support; uses little muscle propulsion
Other	Other locomotor behaviors

Table 24. Body size estimates.

Discrete Categories	Estimated Body Size
Adult male	11 kg.
Adult female with infant on belly	9.62 kg.
Adult female without infant	8.44 kg.
Subadult (all sexes)	5.16 kg.
Juveniles (all sexes)	1.18 kg.

5.3. Results

The red-shanked douc arm-swings approximately 18% of the time it is traveling in the wild (Table 25). Frequency of arm-swing behavior steadily increases as body size decreases (Table 26). In both variants of the data, juveniles arm-swing more than adult males (Tables 27, 28) for discrete categories. When considering all locomotor strides in the continuous GLMM analysis, as body size decreases, there is significant increase in arm-swinging likelihood (Table 29). When considering initial strides, while the directions are identical, the effect loses significance (Table 30). The predicted likelihood each discrete category will use arm-swinging for both all and initial locomotor strides are shown in Figures 13 and 14.

In total, 673 locomotor bouts were analyzed for all age and sex classes (Table 31, 32, 33). The ‘other’ locomotor category has a relatively high count because of behaviors

that ultimately reposition the individual on the branch prior to or after a series of locomotor strides such as a bridge, scoot, or hop—for term definitions see Hunt et al. (1996a). In an effort to be somewhat consistent with existing literature (e.g. Dunham 2015; McGraw 1998b) and for comparability between studies, locomotor categories were kept broad.

Table 25. Frequencies of locomotor behaviors for all age and sex classes.

Quadrupedal	Leap	Arm-Swing	Climb	Drop	Other
35.66 %	18.57%	18.13%	14.41%	7.58%	5.65%

Table 26. Frequencies of locomotor behaviors for each of the discrete body size categories.

	Quadrupedal	Leap	Arm-Swing	Climb	Drop	Other
Adult Male	45.11%	17.93%	9.78%	12.50%	10.32%	4.35%
Adult female with infant	34.48%	15.52%	15.52%	22.41%	10.34%	1.72%
Adult female without infant	33.09%	16.18%	17.65%	17.28%	6.62%	9.19%
Subadult (all sexes)	30.00%	23.33%	21.67%	16.67%	5.00%	3.33%
Juveniles (all sexes)	29.29%	25.25%	34.34%	4.04%	5.05%	2.02%

Table 27. Generalized linear mixed model analysis of all locomotor strides for discrete categories.

	Estimate	Standard Error	Z Value	P Value
Adult Males (Intercept)	-2.85	0.46	-6.23	p < 0.001
Adult Females Carrying Infant	0.96	0.75	1.29	p = 0.20
Adult Females without Infant	0.80	0.52	1.54	p = 0.12
Subadult (All Sexes)	1.17	0.73	1.60	p = 0.11
Juveniles (All Sexes)	1.99	0.77	2.58	p = 0.01

Table 28. Generalized linear mixed model analysis of initial locomotor strides for discrete categories.

	Estimate	Standard Error	Z Value	P Value
Adult Males (Intercept)	-1.99	0.28	-7.24	p < 0.001
Adult Females Carrying Infant	0.53	0.53	0.99	p = 0.32
Adult Females without Infant	0.50	0.34	1.48	p = 0.14
Subadult (All Sexes)	0.61	0.48	1.26	p = 0.21
Juveniles (All Sexes)	0.96	0.40	2.39	p = 0.02

Table 29. Generalized linear mixed model analysis of all locomotor strides using body mass estimates as continuous variables.

	Estimate	Standard Error	Z Value	P Value
Intercept	-0.55	0.62	-0.87	p = 0.38
Body Size	-0.19	0.08	-2.56	p = 0.01

Table 30. Generalized linear mixed model analysis of initial locomotor strides using estimated body masses as continuous data.

	Estimate	Standard Error	Z Value	P Value
Intercept	-0.53	0.75	-0.71	p = 0.475
Body Size	-0.11	0.09	-1.46	p = 0.144

Table 31. Total counts of locomotor strides for each discrete body size category.

Adult male	Adult female	Adult female with baby	Adult female without baby	Juvenile
184	58	272	60	99

Table 32. Total counts of locomotor bouts for each locomotor type for all age and sex classes.

Quadrupedal	Leap	Arm-swing	Climb	Drop	Other
240	125	122	97	51	38

Table 33. Total counts of each locomotor behavior for each of the body size categories.

	Adult Male	Adult female with baby	Adult female without baby	subadult	juvenile	total
Arm- swing	18	9	48	13	34	122
Quadruped	83	20	90	18	29	240
Leap	33	9	44	14	25	125
Climb	23	13	47	10	4	97
Drop	19	6	18	3	5	51
Other	8	1	25	2	2	38
Total	184	58	272	60	99	673

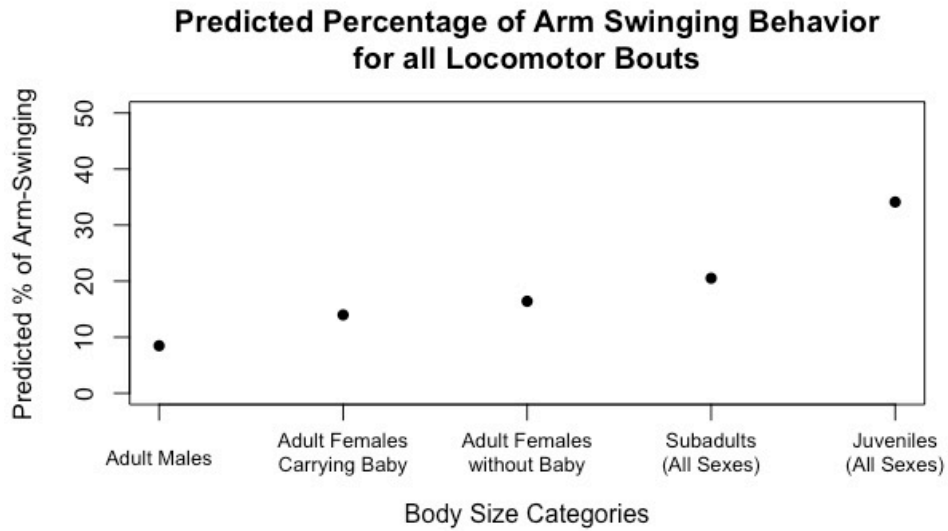


Figure 13. Predicted percentage of arm-swinging behavior for all locomotor bouts.

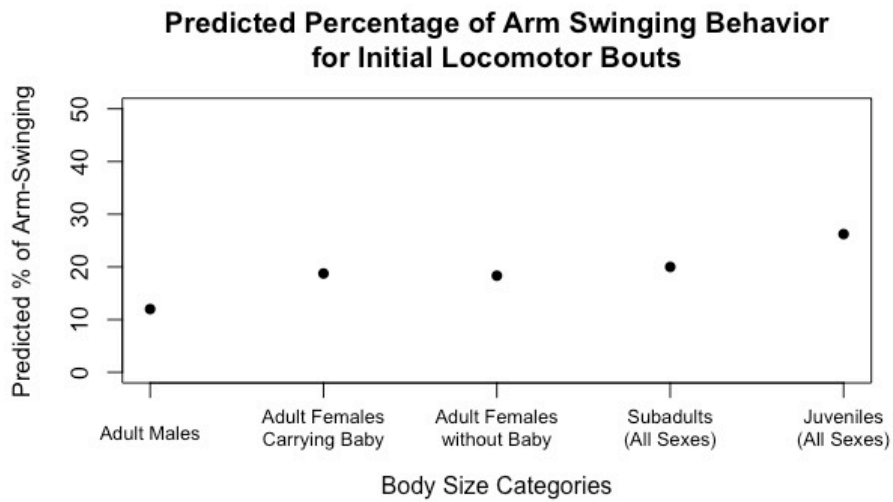


Figure 14. Predicted percentage of arm-swinging behavior for initial locomotor bouts.

5.4. Discussion

The results show that overall, *P. nemaesus* exhibits higher proportions of arm-swinging than most other colobines, but it is not likely a function of an increased body size because arm-swinging is most frequently used in smaller bodied individuals, i.e. juveniles. These results are consistent with previous work at the EPRC that show that young doucs perform suspensory behavior more than adults. It is important to note, however, that in most cercopithecids, juveniles exhibit higher diversity of all locomotor categories, including more frequent suspensory behaviors (Workman and Covert 2005). Similarly, Dunham (2015) found black and white colobus (*Colobus angolensis palliatus*) juveniles to have a more diverse locomotor repertoire than adults, including juveniles using bimanual suspension—unlike the adults. This variance can be explained because juveniles have more flexible joints, are not inhibited by a larger body size, and are fully able to exploit all areas of their environment (Dunbar and Badam 1998). While it is not entirely surprising that juveniles use a higher proportion of arm-swinging behavior, it is surprising that a relative abundance of arm-swinging persists into adulthood unlike so many other colobines.

One potential explanation of arm-swinging in adult red-shanked doucs is that this behavior continues because of postural and environmental variables. Wright et al. (2008) proposed that because gibbons and doucs are moving in similar ways, there are probably

similar environmental constraints for the two taxa. One benefit of suspensory postures includes making terminal, flexible substrates more accessible (Avis 1962; Grand 1972). Furthermore, accessing food from below the branch increases the available feeding sphere (Grand 1972). One study focusing on the feeding posture and scapular morphology identified a few aspects of the scapula of some colobines, *Ptilocolobus badius* and *Colobus polykomos*, to be indicative of greater arm abduction and elevation, particularly when compared to cercopithecines (Dunham et al. 2016). This forelimb abduction manifests primarily through a superior retrieval of food when foraging. If *Pygathrix* is using below-branch locomotion as a method of accessing terminal branches, a feeding posture study is warranted. In this study, arm-swinging appeared to be preferred on medium size branches in the main canopy of primary forest. In secondary forest, the vegetation is quite dense, making any type of quick movement difficult.

At present, there are no studies looking at the ontogenetic locomotor differences in the hylobatids; it would be interesting to see if the results are comparable and if the juveniles are arm-swinging more than the adults. Given the similarities in the kinetics and kinematics between doucs and gibbons, perhaps the juvenile gibbons arm-swing more than adults (which arm-swing approximately 74 - 80% of the time during travel bouts) (Andrews and Groves 1976; Gittins 1983). Future research is necessary to determine why arm-swinging behavior is persisting into the adulthood of *Pygathrix*. Furthermore, the current Endangered (Vu Ngoc Thanh et al. 2008b) status of *P. nemaus* emphasizes the importance of understanding how this species interacts with its environment to safeguard the preservation of this taxon.

CHAPTER VI

ARM-SWINGING AND HABITAT USE OF THE RED-SHANKED DOUC LANGUR (*PYGATHRIX NEMAEUS*) IN THE SON TRA NATURE RESERVE, VIETNAM

6.1. Introduction

In the last forty years, a few seminal papers have investigated the relationship between primate locomotion and habitat structure (e.g. Fleagle and Mittermeier 1980a; Gebo and Chapman 1995; McGraw 1998c). These studies have largely attempted to understand which locomotor behaviors correspond with certain forest variables and often incorporate morphological factors, such as body size, into the analysis. In particular, the evolution of below-branch-locomotion (also called suspensory locomotion) is often explained from field studies as an adaptation to support an increased body size in an arboreal environment (e.g. Cant 1992; Fleagle and Mittermeier 1980a; Napier and Napier 1967). Furthermore, below-branch locomotion increases the feeding sphere by making smaller, unstable, terminal substrates more accessible (Grand 1972). While it is difficult to tease apart environmental variables and morphology, it is important to do so to eliminate any confounding factors.

One group of monkeys that have undergone extensive investigation into their locomotor behavior and habitat use are the colobines. Colobinae represents a group of folivorous monkeys found in Africa and Asia (Davies and Oates 1994; Fleagle 2013) and are well known for their arboreal habitat exploitation. In general, colobines are typically considered to be arboreal quadrupeds that engage in a great deal of leaping with few

exceptions (e.g. McGraw 1998b; Mittermeier and Fleagle 1976; Zhu et al. 2015). However, one group of colobines, the douc langurs (*Pygathrix spp.*), deviates from others. The red-shanked douc (*P. nemaeus*) has been observed engaging in high proportions (46% of travel time) of suspensory behavior in captivity at the Endangered Primate Rescue Center (hereafter, EPRC) (Byron and Covert 2004). This proportion is distinct from other colobines, for example the western red colobus (*Ptilocolobus badius*), that only uses suspensory locomotion 2.9% of the time (McGraw 1998b).

The arm-swinging of *Pygathrix* is remarkably similar to that of the hylobatids (gibbons). Kinematically, the doucs and gibbons move in similar ways, differing in that gibbons use quicker, more continuous arm-swinging bouts (Wright et al. 2008). Kinetically, doucs and gibbons also move in a similar way by using a pendulum motion to propel the trunk forward, but with doucs using larger side to side movements (Granatosky 2015). Gibbons are typically designated as obligate brachiators (Bertram 2004) and to denote these subtle differences, we use arm-swinging to describe *Pygathrix*'s bimanual locomotor behavior rather than brachiation. In addition, the New World atelines are known for their suspensory locomotor behavior, however, they typically assist any arm-swinging with their prehensile tail (Napier and Napier 1967).

Byron and Covert (2004) compared the red-shanked douc and two other species of Asian colobines, Delacour's langur (*Trachypithecus delacouri*) and the Hatinh langur (*Trachypithecus laotum hatinhensis*) and found the red-shanked douc to use suspensory locomotion whereas the other two used none. All three species are housed in similar enclosures which reasonably rules out considering this behavior a captive anomaly. Later,

an additional study incorporated the grey-shanked douc and found they also arm-swing at comparable proportions (56% of the time) (Wright et al. 2008). One study wild-based on the socioecology of the black shanked douc also collected data on their locomotion and found that they arm-swing 9.7% of the time (Rawson 2009).

It remains unclear why *Pygathrix nemaeus* incorporates such high proportions of arm-swinging behavior into their locomotor repertoire. After comparing the suspensory behavior of doucs and gibbons, Wright et al. (2008:1476) concluded, “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.” This inference projects that the arm-swinging of doucs and the brachiation of gibbons is likely occurring on (at least some of the following) similar substrate sizes, substrate angles, forest strata, and forest type. The agile gibbon (*Hylobates agilis*) has previously been observed using brachiation 74% of the time and more frequently on medium-sized substrates (branches), followed by larger substrates (boughs), and then smaller substrates (twigs) (Gittins 1983). However, another hylobatid, the siamang (*Symphalangus syndactylus*), which is nearly twice the size of other gibbons (Fleagle 2013) has been observed using brachiation 51% of the time (while traveling) and more frequently on boughs, followed by branches, then twigs (Fleagle 1976).

Given the resemblance in movement between the gibbons and the doucs, we speculate that one of the reasons doucs are arm-swinging is because of similarities of habitat use. Here, we attempt to identify patterns of habitat use corresponding to arm-swinging of the red-shanked douc. We specifically try to answer the following research

question: to what extent does habitat use influence arm-swinging behavior of *Pygathrix nemaeus*? Are these behaviors similar to what has previously been reported with gibbons? Or those of the siamang? Following the suggestion of Wright et al. (2008) we predict arm-swinging will occur significantly more on horizontal substrates, in the main canopy, on medium sized substrates, and in old-growth forest, similar to that of gibbons.

6.2. Methods

Son Tra Nature Reserve is confined to a peninsula abutting Da Nang, Vietnam. The forest in Son Tra is made up of primary [old-growth] moist evergreen forest (approximately 400 ha), dry secondary [new-growth] forest (approximately 2,611 ha, and grassland (Sourcebook 2004; Van Peenen et al. 1971). The trees have an average height of 9.34 (\pm 3.52) meters (Ulibarri 2013). Mount Son Tra is the highest peak within the reserve with an elevation of 696 m. The coastal region of Vietnam where Son Tra Nature Reserve is located, is subject to two primary seasons; the monsoon (wet) season and the dry season (Van Peenen et al. 1971). Data were collected between November 4th, 2016 and March 13th, 2017, which spans both seasons and avoids seasonality biases.

Red-shanked doucs are the only colobine on the peninsula and are accustomed to humans. There is a road that circles the peninsula and crosses the top of the peak that photographers use to photograph the monkeys on a daily basis. The doucs are often found close to the road because they feed extensively on a species of morning glory (*Ipomoea eberhardtii*). Because they are often found along the road, this vantage point was used for data collection. Data were collected by filming the doucs with a Canon Vixia handheld camera or a Canon 70D DSLR with a 250mm lens. Approximately 90 hours of footage

was recorded. Filming along the road offered both benefits and limitations. A benefit is that the road typically provided a vantage point that allowed us to see a greater distance over the forest and follow the doucs with the lens from further away. One limitation is that there may be some potential edge effects that bias the data, but given the exceptionally fragmented reserve, this issue is largely unavoidable. This bias would be the doucs changing their locomotor behavior as a result of the discontinuous canopy. Furthermore, it was not possible to see the doucs from below the closed canopy on the forest floor. Entering the forest was problematic because most of the forest is growing on steep rocky terrain that would likely require safety gear to traverse.

It was not possible to distinguish groups or individuals' day to day so filming began once a group was found and filming stopped once all individuals moved out of sight or were no longer visible. After a group left visible range a new group was located and filming was resumed. After completing footage collection in Da Nang, data was then extracted and coded into Microsoft Excel. The following information was recorded for each behavioral observation: clip number, individual ID (for that clip), locomotion (Table 34), and environmental data (Table 35). Substrate sizes were always estimated in relation to douc hand size and a reference scale was kept offscreen for comparative purposes. Forest type was determined by relative tree height and relative density of the vegetation.

Table 34. Ethogram of locomotor behaviors (Hunt et al. 1996a).

Arm-Swing	Hand over hand progression, propelling the trunk forward
Quadrupedal run/walk	Four limb sequence walk/ run across substrate
Leap	Four limbs leave substrate for a period of time while traveling using significant muscle propulsion
Climb	Hand over hand, foot over foot diagonal sequence propulsion, usually going up
Drop	Release from a support by falling down to another support; uses little muscle propulsion
Other	Other locomotor behaviors

Table 35. Environmental data (Fleagle 1976; McGraw 1998b; McGraw 1998c).

Substrate angle	Horizontal
	Oblique
	Vertical
Substrate	Bough – large supports about 10 cm + in diameter
	Branch – medium sized, between 2 – 10cm in diameter
	Twig(s) – less than 2cm in diameter
Forest Type	Old Growth
	New Growth
Forest Strata	Ground
	Shrubs and saplings – small easily bendable trees
	Main canopy
	Top of canopy – emergent layer

All data analyses were completed using the R packages *tidyr* (Wickham and Henry 2017), *readxl* (Wickham 2015), *lme4* (Bates et al. 2015), and *glmm* (Knudson 2018). Data were continuously extracted from all footage because of the variability of clip length. To control for any autocorrelation that might arise from a continuous sampling method, the data were analyzed in two permutations. First, the data were analyzed using all locomotor strides. Second, the data were analyzed by sampling out only the initial stride of each

locomotor bout. Clip number and individual ID were combined to create a unique identifier for each line of behavior. This unique ID became a random effect which required the data (both variants) to be analyzed via Generalized Linear Mixed Model (GLMM) for all environmental variables. We also identified the proportion of time spent arm-swinging on each of the categories of environmental factors. Prior to commencing the data analysis, lines of data were removed if an environmental variable was observed fewer than 10 times. The following lines of data were removed: forest floor, shrubs and saplings, and any out-of-sight or unknown substrate size or substrate angle.

6.3. Results

Vertical supports are significantly less likely to be used for arm-swinging than horizontal supports and oblique supports are slightly more likely to be used (but not significantly more so) than horizontal supports for both initial and all strides (Tables 36, 37). Twigs are significantly less likely to be used for arm-swinging for initial and all locomotor strides, while branches are only significantly more likely to be used in all strides (Tables 38, 39). Arm-swinging is significantly less likely to occur on the top of canopy (Tables 40, 41) for all and initial strides. Finally, arm-swinging is significantly less likely to occur in new-growth forest for all strides (Table 42) but not for initial strides (Table 43). Arm-swinging occurred most frequently in old growth forests (Table 44), in the main canopy (Table 45), on horizontal and oblique substrates (Table 46), and on branch and twig-sized substrates (Table 47). When evaluating these results with a Bonferroni adjusted p-value (0.0125), only forest strata remains significant after adjusting the p-value for the Bonferroni correction.

Table 36. Generalized linear mixed model analysis of substrate angle and arm-swinging for all strides.

	Estimate	Standard Error	Z Value	P Value
Horizontal (Intercept)	-1.85	0.37	-5.06	p > 0.001
Oblique	0.40	0.36	1.10	p = 0.27
Vertical	-3.15	1.10	-2.85	p = 0.004

Table 37. Generalized linear mixed model analysis of substrate angle and arm-swinging for initial strides.

	Estimate	Standard Error	Z Value	P Value
Horizontal (Intercept)	-1.07	0.20	-5.23	p > 0.001
Oblique	0.18	0.29	0.63	p = 0.532
Vertical	-2.45	1.03	-2.37	p = 0.018

Table 38. Generalized linear mixed model analysis of substrate size and arm-swinging for all strides.

	Estimate	Standard Error	Z Value	P Value
Bough (Intercept)	-2.96	0.70	-4.25	p > 0.001
Branch	1.45	0.69	2.12	p = 0.034
Twig	0.53	0.77	0.70	p = 0.487

Table 39. Generalized linear mixed model analysis of substrate size and arm-swinging for initial strides.

	Estimate	Standard Error	Z Value	P Value
Bough (Intercept)	-1.78	0.51	-3.52	p > 0.001
Branch	0.80	0.53	1.50	p = 0.133
Twig	0.35	0.58	0.61	p = 0.544

Table 40. Generalized linear mixed model analysis of forest strata and arm-swinging for all strides.

	Estimate	Standard Error	Z Value	P Value
Main Canopy (Intercept)	-1.55	0.30	-5.14	p > 0.001
Top of Canopy	-1.93	0.66	-2.94	p = 0.003

Table 41. Generalized linear mixed model analysis of forest strata and arm-swinging for initial strides.

	Estimate	Standard Error	Z Value	P Value
Main Canopy (Intercept)	-0.96	0.16	-6.17	p > 0.001
Top of Canopy	-1.37	0.50	-2.77	p = 0.006

Table 42. Generalized linear mixed model analysis of forest type and arm-swinging for all strides.

	Estimate	Standard Error	Z Value	P Value
Old Growth (Intercept)	-1.50	0.35	-4.26	p > 0.001
New Growth	-1.03	0.53	-1.97	p = 0.049

Table 43. Generalized linear mixed model analysis of forest type and arm-swinging for initial strides.

	Estimate	Standard Error	Z Value	P Value
Old Growth (Intercept)	-1.03	0.19	-5.37	p > 0.001
New Growth	-0.36	0.31	-1.16	p = 0.246

Table 44. Proportion of arm-swinging in forest type.

Old Growth	New Growth
61% (n=75)	39% (n=48)

Table 45. Proportion of arm-swinging in the forest strata.

Main Canopy	Top of Canopy
96% (n=118)	4% (n=5)

Table 46. Proportion of arm-swinging on different substrate angles.

Horizontal	Oblique	Vertical
62% (n=76)	37% (n=46)	1% (n=1)

Table 47. Proportion of arm-swinging on different substrate sizes.

Bough	Branch	Twig
4% (n=5)	63% (n=78)	33% (n=40)

6.4. Discussion

By all accounts the red-shanked douc is using arm-swinging in the expected categories of forest strata, forest type, substrate size, and substrate angle. Both variants of the data are depicting similar stories, despite losing some significance for initial strides on branches. Because of the overall consistency between the models for the two variants of data, we tentatively surmise that autocorrelation is not an effect of the overall analysis.

More often than not, arm-swinging takes place in old growth forest and in the main canopy. Typically, old growth forests are the standard habitat for colobines and new growth is a largely a result of anthropogenic influences (Davies and Oates 1994). What is interesting about these results is that the doucs are still clearly capable of arm-swinging in

new growth forest. The tops of canopies, or the emergent layer, leaves the doucs (particularly juveniles) exposed to potential arboreal predators (Fam and Nijman 2011) which could dissuade the doucs from traveling in that layer. Substrate angle follows an expected norm with vertical substrates being virtually nonexistent supports for arm-swinging. The most common substrate sizes used by the doucs for arm-swinging are branches, followed by twigs then boughs.

In captivity at the EPRC the doucs are housed in enclosures that are constructed of bamboo poles that are approximately 2 – 8 cm in diameter (Wright et al. 2008). Substrates that are branch sized (2 – 10 cm in diameter) were the most common support size for arm-swinging in the wild, which could help explain why the proportions of arm-swinging are so high in captivity. Similar data on substrate size has also been collected on hylobatids and spider monkeys. Gittins (1983) identified the agile gibbon to brachiate 32% of the time on boughs, 51% on branches, and 17% of the time on twigs. Fleagle (1976) recorded that during travel, the siamang brachiated most frequently on boughs (57%), followed by branches (41%), then twigs (2%). Locomotion during travel is differentiated from foraging as travel that occurs over greater distances, to and from feeding sites, and between major food sources. Locomotion during foraging was more similar to that of the agile gibbon with branches being the most common (50%), followed by boughs (42%), then twigs (8%) (Fleagle 1976).

Fleagle and Mittermeier (1980a) report that 38.6% of the locomotor bouts of *Ateles paniscus paniscus* were arm-swinging and about 70% of this type of locomotion took place on branches, and about 30% on twigs, with virtually none on boughs. In the present

study, branches were also the most common substrate used for the doucs (63%), but the doucs differ from the gibbons in that they then use twigs more frequently (33%) which is more consistent with the behavior of the spider monkey. Spider monkeys often accompany their suspensory behavior with the use of their prehensile tail (though not always), which aids in distributing their weight across a wider surface (Fleagle and Mittermeier 1980a). These results are consistent with what Mittermeier (1978) previously reported for *Ateles paniscus* in that suspensory locomotion was most common on branches, twigs, then boughs. *Presbytis potenziani* (the Mentawai langur) only uses arm-swinging about 1% of the time (4/388 counts) and only on large boughs (Fuentes 1996) despite the Mentawai langur being much more closely related to the doucs (both are in the Colobinae subfamily, whereas *Ateles* is in a different infraorder) than the spider monkey.

Another colobine, *Rhinopithecus avunculus* (the Tonkin snub-nosed monkey), arm-swings 5.23% in the wild and does so most frequently on branches (77.78%), twigs (13.33%), boughs (6.67%), then tree trunks (2.22%) (Le Khac Quyet 2014). These proportions follow a similar pattern to the red-shanked douc albeit the Tonkin snub nosed monkey arm-swings much less frequently. Both *R. avunculus* and *P. nemaesus* are found in Vietnam though they have non-overlapping geographic ranges (Rowe and Myers 2016).

All of the aforementioned primates (the agile gibbon, siamang, the spider monkey, the Tonkin snub-nosed monkey, and the douc) live in different geographical locations (Rowe and Myers 2016) thus putting limitations on broad conclusions. However, perhaps some of the same selective pressures that have acted on the spider monkey to adopt arm-swinging behaviors might have also acted on the doucs considering the similarities in

substrate use. Overall the doucs appear to be using arm-swinging in expected, secure ways in this environment in terms of forest strata, substrate angle, and forest type. The subtle differences in arm-swinging and brachiation as previously described (Granatosky 2015; Wright et al. 2008) might explain the differences in substrate size preference.

The three species of *Pygathrix* have virtually no overlap in their geographical ranges (Rowe and Myers 2016) thus implying there is at least some variation between each of their habitats. Despite that difference in range, all three species of *Pygathrix* have similarly shaped scapula (Bailey and Pampush 2015) (which is integral to below branch locomotion) and are thus all likely moving in similar ways in their respective environments. Furthermore, the information presented here can contribute to the conservation of the Endangered red-shanked douc (Vu Ngoc Thanh et al. 2008b) by providing agencies with information essential to their survival in a given environment.

CHAPTER VII

CONCLUSION

The goal of this dissertation research was to provide insight into the general question *why arm-swing?* All three species of douc langur have a similarly shaped scapula. This information suggest that they may be using their shoulder in similar ways. Within the primates samples, the douc langur scapula generally falls intermediary in shape between quadrupedal cercopithecids and brachiating apes. Doucs share features with both groups, which may explain why they consistently use both forms of locomotion in their repertoire. This dissertation also shows some support that it is possible to predict locomotor capabilities based on the distance the acromion process projects past the glenoid fossa in primates that use their forelimbs for locomotion.

This dissertation also presented the first study to focus exclusively on douc locomotion in the wild. Results show that the arm-swinging behavior is in fact occurring in the wild but it is likely not a function of increased body size; rather arm-swinging is more prevalent among the younger/ smaller individuals. In general, most juvenile primates have greater variation in their locomotor repertoire (including suspensory behavior) because of their flexible joints and small body size (Dunbar and Badam 1998). Furthermore, this research identified arm-swinging with corresponding habitat variables. The red-shanked doucs prefer old growth forest, in the main canopy, and branch-sized, horizontal substrates when arm-swinging.

At this time, there is only one zoo in the United States that houses the douc langurs. This is primarily because their diet is difficult to replicate and there is so little existing information on this primate. Locomotor studies are critical for zoo programs because they inform habitat and enclosure design. Proper habitat structures ensure that these primates are living in conditions as similar as possible to their natural environment, which in turn reduces environmental stressors. Furthermore, zoos are one of the best tools for public education in the United States, especially in regards to exotic wildlife.

It is an unfortunate reality that large swaths of habitat can rarely be protected to fully conserve a species or genus. However, understanding how an animal moves in a relatively undisturbed environment for general travel and food acquisition is pivotal to ensure the most essential parts of their habitat is protected. These primates are subject to an ever-changing environment as a result of deforestation, increased agriculture production, mining, and hunting; all of which are a direct result of human influence. The more deforestation occurs, the more arboreal primates have to adapt their locomotor patterns. This project helped identify how these monkeys use their habitat. The red-shanked douc langur is currently classified as Endangered by the International Union for the Conservation of Nature (IUCN) (Vu Ngoc Thanh et al. 2008b). The sister taxa, *P. cinerea* is classified as Critically Endangered and *P. nigripes* is classified as Endangered (Rawson et al. 2008; Vu Ngoc Thanh et al. 2008a). Given the close-relatedness of these species, the information gathered from this project can hopefully be used in future conservation action plans for the genus.

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