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Cover: Northern white-cheeked gibbon, female (*Nomascus leucogenys*). Photo: T. Nadler.

The critical status of the Delacour's langur (*Trachypithecus delacouri*) and the call for a National Action Plan

Tilo Nadler

Endangered Primate Rescue Center, Cuc Phuong National Park,
Nho Quan District, Ninh Binh Province, Vietnam. <t.nadler@hust.edu.vn>

Key words: Delacour's langur, *Trachypithecus delacouri*, status, distribution

Summary

The Delacour's langur (*Trachypithecus delacouri*) is one of the three primate species endemic to Vietnam, and listed as 'Critically Endangered' (IUCN 2015). In addition, this species has been continuously included in the biennial list of "The World's 25 Most Endangered Primates" (Mittermeier et al. 2000; 2012), since the lists inception in 2000.

For an assessment of the current status of the species, 20 surveys were carried out in all nine areas where populations of the species remain.

The results of the surveys show a similar pattern to surveys undertaken over the last decade: a continued dramatic decrease in many subpopulations due to poaching. Only the population at Van Long Nature Reserve is the exception, growing steadily following a complete hunting ban supported by a community based protection unit, and intensive work by the Management Board. Van Long Nature Reserve has high awareness and support in the surrounding communes as a result of a 15 year long conservation project supported by Frankfurt Zoological Society.

The surveys showed that eight subpopulations of the Delacour's langur have been eradicated during the last decade.

From data gathered during the latest surveys, the current total population is now estimated at 234-275 individuals in 8 subpopulations. The two largest populations occur in Van Long Nature Reserve and in a planned extension area of the reserve.

As the reserve and the planned extension area are administrated by two separate provincial authorities, the langurs occurring here have been identified as occurring in two separate populations; however they do in fact form one population.

All other subpopulations surveyed are already too small to survive long-term.

Thus the most important conservation action for the species would be the extension of Van Long Nature Reserve. The size of the extended nature reserve and the existing habitat conditions could support a large viable population.

An improvement of protection for all subpopulations outside Van Long Nature Reserve in order to secure their survival is not feasible, due to the lack of adequate protection or political will to improve protection.

The translocation of groups or individuals from very small populations is also not a feasible option. Translocation requires a very high personal resource, technical and financial investment has little proven success and would need to be undertaken in areas with very difficult access and terrain.

The Endangered Primate Rescue Center runs a successful captive breeding program for the species. The goal is the reintroduction of captive bred animals into a safe habitat. A pilot project has already been successfully undertaken by the EPRC, with the first reintroduction of captive bred individuals into Van Long Nature Reserve. The establishment of a second viable population of the species would be a priority for conservation. There also exists a possibility for another reintroduction into the recently established World Heritage Site "Trang An Scenic Landscape Complex" in Ninh Binh Province.

These surveys showed that the priority for a conservation intervention should be the extension of Van Long Nature Reserve and a feasibility study for the reintroduction of captive bred individuals

into the “Trang An Scenic Landscape Complex”, thus establishing a second population in an area with higher protection.

Conservation activities for the species are recommended, and the development of a National Action Plan for one of the Vietnamese endemic primate species would provide the basis to support the survival of the species.

A further decrease of the number of individuals with extinction in foreseeable future would be a depressing shame for the country and a great and irrecoverable loss for the world.

Tình trạng nguy cấp của loài Voọc Mông Trắng (*Trachypithecus delacourii*) và sự cần thiết của một kế hoạch hành động bảo tồn cấp quốc gia

Tóm tắt

Voọc Mông trắng (*Trachypithecus delacourii*) là một trong ba loài linh trưởng đặc hữu của Việt Nam, loài này được liệt vào danh sách những loài cực kỳ nguy cấp của IUCN (2015). Từ năm 2000, loài liên tục nằm trong danh sách “25 loài linh trưởng nguy cấp nhất thế giới” (Mittermeier và cộng sự 2000; 2012). Nhằm đánh giá hiện trạng bảo tồn, 20 đợt khảo sát thực địa tại 9 điểm phân bố đã được thực hiện. Kết quả cho thấy các tiểu quần thể suy giảm nhanh do săn bắn, bẫy bắt. Ngoại trừ quần thể ở Khu bảo tồn thiên nhiên đất ngập nước Vân Long có số lượng tăng trưởng ổn định. Quần thể ở Vân Long phát triển ổn định do việc thực thi pháp luật khá tốt với sự hỗ trợ của đội ngũ nhân viên bảo vệ rừng tại cộng đồng và nỗ lực của ban quản lý khu bảo tồn. Khu bảo tồn thiên nhiên đất ngập nước Vân Long được sự quan tâm, ủng hộ cao của các cấp chính quyền cùng nhân dân vùng đệm với sự hỗ trợ của Hội Động vật học Frankfurt trong suốt 15 năm qua.

Kết quả những đợt khảo sát cho thấy 8 tiểu quần thể loài Voọc Mông trắng đã bị xóa sổ trong 10 năm vừa qua. Tổng số cá thể còn lại giao động từ 234 đến 275 thuộc 8 quần thể. Hai quần thể lớn nhất tại Khu bảo tồn thiên nhiên đất ngập nước Vân Long và khu vực dự định mở rộng của khu bảo tồn này. Tuy nhiên, hai quần thể này có thể xem là một vì điều kiện địa lý liên kề nhau. Điểm khác biệt chỉ là địa giới hành chính thuộc sự quản lý của hai tỉnh Ninh Bình và Hòa Bình.

Những tiểu quần thể đã được khảo sát lần này có kích thước rất nhỏ nên khó có thể tồn tại lâu dài. Vì vậy, hoạt động bảo tồn quan trọng là cấp thiết mở rộng Khu bảo tồn thiên nhiên đất ngập nước Vân Long. Diện tích của khu bảo tồn sau mở rộng có thể hỗ trợ một quần thể Voọc Mông trắng lớn được tồn tại và phát triển. Việc cải thiện tình trạng bảo vệ các tiểu quần thể nhỏ khác dường như không khả thi. Chưa có giải pháp bảo vệ hiệu quả bởi còn thiếu sự quan tâm của chính phủ nhằm cải thiện các hoạt động bảo vệ và bảo tồn loài.

Giải pháp di dời các tiểu quần thể nhỏ cũng không khả thi. Bởi vì việc di dời sẽ đòi hỏi kinh phí, kỹ thuật và nhân lực rất tốn kém, trong khi ít có những thành công tương tự được chứng minh. Mặt khác, việc thực hiện di dời trong tình trạng khó tiếp cận trên địa hình núi đá cũng là trở ngại rất lớn. Hiện nay, Trung tâm Cứu hộ Linh trưởng Nguy cấp đang thực hiện thành công chương trình cứu hộ, chăm nuôi và sinh sản. Mục tiêu của chương trình là cho sinh sản và thiết lập lên những bầy đàn ổn định để có thể tái thả chúng trở về môi trường sống tự nhiên có điều kiện an toàn. Một dự án thử nghiệm đã thành công thả vào tự nhiên tại Khu bảo tồn thiên nhiên đất ngập nước Vân Long một số cá thể được sinh trưởng trong điều kiện nuôi nhốt. Việc tiếp tục cho sinh sản, thiết lập các quần thể ổn định phục vụ chương trình hòa nhập vào tự nhiên là một trong những ưu tiên bảo tồn loài. Chương trình tiếp tục tái hòa nhập Voọc Mông trắng vào tự nhiên cũng đang được đề xuất đưa về Khu Di sản thế giới Tràng An, tỉnh Ninh Bình.

Kết luận, những hoạt động bảo tồn ưu tiên cho loài cần thực hiện chính là việc mở rộng Khu bảo tồn thiên nhiên đất ngập nước Vân Long và nghiên cứu tiên khả thi cho dự án tái hòa nhập loài này về Khu Di sản thế giới Tràng An, nơi có điều kiện tổ chức hoạt động bảo vệ tốt.

Các kế hoạch hành động bảo tồn loài cần được đề xuất và cấp thiết xây dựng kế hoạch hành động quốc gia chung và đối với loài linh trưởng này là một trong hai loài linh trưởng đặc hữu và quý hiếm của Việt Nam. Những hoạt động bảo vệ và bảo tồn cấp thiết sẽ là cơ hội cho sự tồn tại của loài.

Những tổn thất về mặt quần thể sẽ dẫn đến nhiều mối nguy hại và gây nên tuyệt chủng của loài và đây sẽ là sự mất mát về không chỉ cho Việt Nam mà cho cả thế giới.

Introduction

The Delacour's langur (*Trachypithecus delacouri*) is one of three primate species endemic to Vietnam, and listed as 'Critically Endangered' (IUCN 2015). Since the creation in 2000 of the biennial listing of a consensus of 25 primate species considered to be the most in need of urgent conservation measures, the Delacour's langur has been continuously listed. Based on the low number of individuals, the fragmented population and the dramatic decrease the species counts to "The World's Top 25 Most Endangered Primates" (Mittermeier et al. 2000; 2012).

For an assessment of the current status of the species, 20 surveys were carried out between 2012 and 2015 in all nine areas where populations of the species remain.

To illustrate the status and the dramatic decline of the species over a longer period an overview from the last decade of the 20th century is compiled.

The synopsis of the status shows the critical situation of the species. Conservation activities for the species are recommended, and the development of a National Action Plan for one of the Vietnamese endemic primate species would provide the basis to support the survival of the species.

Distribution and Status of Delacour's langurs in the wild

Distribution and Status of the species before 2000

The Delacour's langur was discovered during one of the expeditions led by Jean Delacour in 1930. The scientific description by Osgood (1932) was based on two animals, a male and a female hunted by locals and purchased in Hoi Xuan, a town close to the later established Pu Luong Nature Reserve, the area which is most probably the origin of the animals.

There exists no information about the species until the first living individuals were observed in 1987 in Cuc Phuong National Park (Ratajszczak, 1990).

This discovery was the background for Frankfurt Zoological Society to start a primate program in Cuc Phuong National Park to gather information about the species: status, distribution and biology.

With the start of the VIETNAM PRIMATE CONSERVATION PROGRAM in 1993 information from locals has been collected and comprehensive surveys conducted to locate populations of the species and to estimate the numbers of individuals. A first overview about the distribution and status noted 10 populations with a total of 121-186 individuals (Nadler, 1996). Following surveys state this information more precisely and resulted in the discovery of 19 subpopulations in a restricted area of northern Vietnam, covering about 5000 km² (Fig. 1). But the area of occurrence comprised only about 400 km² (Fig.2).

Taken from these surveys the total of all populations was estimated at 49-53 groups and 270-302 individuals (Nadler et al. 2003) (Table 1, Fig. 2).

In three areas where Delacour's



Fig.1. Distribution area of the Delacour's langur (*Trachypithecus delacouri*).

langur occurred in the past the species was already eradicated by the 1990s, following information

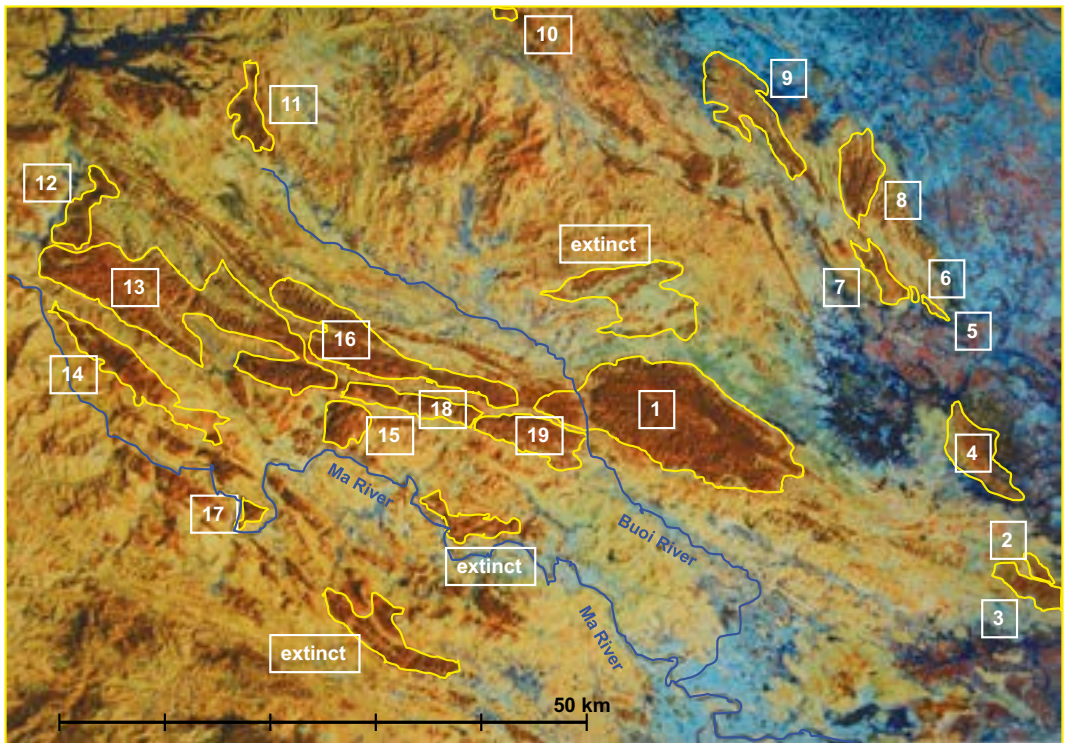


Fig.2. Areas with Delacour's langur populations 1990-2000.

Table 1. Number of groups and individuals of Delacour's langurs in the subpopulations before 2000.

provided by local people.

No.	Locality	Protection status	Groups	Individuals
1	Cuc Phuong National Park	National Park (1962)	4-5	20-25
2	Yen Mo mountain range	non	2	10
3	Bim Son mountain	non	4-5	14-18
4	Hoa Lu – Tam Coc	Nature Reserve (1996)	3	14
5	Van Long area (eastern part)	Nature Reserve (2001)	4	35-40
6	Van Long area (central part)	Nature Reserve (2001)	1	7
7	Van Long area (western part)	Nature Reserve (2001)	1	4-5
8	Lac Thuy – Kim Bang	non	1-2	20
9	Huong Son mountain	Nature Reserve (1993)	6	27
10	Roc mountain	non	1	2
11	Phu Vinh mountainous area	non	2	15
12	Mai Chau mountainous area	non	3	15

13	Pu Luong Nature Reserve (NE-part)	Nature Reserve (1999)	5-7	30-36
14	Pu Luong Nature Reserve (SW-part)	Nature Reserve (1999)	2	10
15	Northern Ba Thouc mountainous area	non	2	9-11
16	Ngoc Son mountainous area	Nature Reserve (2006)	1	5
17	Thiet Ong mountain	non	1	11
18	Nui Boi Yao mountainous area	non	4	17-27
19	Thach Thanh District	non	1	5
	TOTAL		49-53	270-302

Most of the animals occurred in small populations which are very sensitive to any impacts and in particular poaching. (Table 2). About half of all discovered populations (10) occurred in unprotected

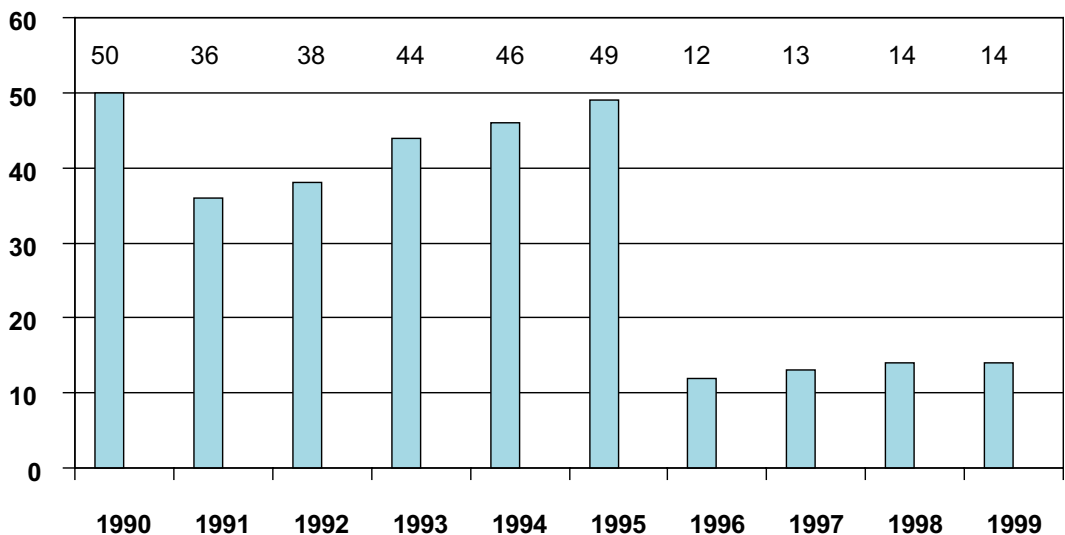
Table 2. Classification and numbers of individuals in subpopulations 1990 -2000.

areas (Table 1). The protection level in protected areas is mostly low, but still under control of the Forest Protection Departments. In unprotected areas there is no control over hunting, and the animals are under high pressure.

Number of individuals in one subpopulation	1-10	11-20	21-30	> 30
Number of subpopulations	8	6	3	2
Number of individuals in these subpopulations	52-55	89-93	63-79	65-75
Percent of individuals of the total population in these subpopulations	~20%	~30%	~25%	~25%

To get an impression of the hunting pressure, the number of hunted Delacour's langur in the distribution area was recorded (Table 3). This list is not complete, because some hunters were not

Table 3. Hunted Delacour's langur in one decade.



found, some didn't remember the exact numbers, and some were afraid to give information. However, these numbers are alarming enough and the recorded total over a period of ten years amounts to 316 individuals, an annual loss of more than 30 individuals.

Since 1996, a clear decline has begun, which has been influenced by the breakdown of some subpopulations and the complete disappearance of langurs in some areas. Based only on the known hunted langurs, the population has lost 50-55% during the decade 1990 to 2000.

Distribution and Status of the species 2000 – 2010

With additional surveys in the first decade of the 21st century the total number of recorded individuals increased slightly. The number of groups is 50-57 and the number of individuals 281-317. The increased total number of langurs resulted in the development of the population in Van Long Nature Reserve, the area under special protection through the Vietnam Primate Conservation Program, which included additional education and awareness programs for the surrounding communes of the area. The distribution of animals within subpopulations during this period indicates a reduction in the occurrence of larger populations compared to the previous decade. (Nadler 2004) (Table 4).

Table 4. Classification and numbers of individuals in subpopulations 2000-2010.

Number of individuals in one subpopulation	1-10	11-20	21-30	> 30
Number of subpopulations	7	8	2	2
Number of individuals in these subpopulations	48-50	119-138	44-54	70-75
Percent of individuals of the total population in these subpopulations	~17%	~43%	~17%	~23%

During this decade a number of small populations were eradicated. The exact years of extirpation cannot be verified. The information is based on interview surveys of local villagers, who indicated that the last sighting or record of the species was often several years ago. Therefore these small populations are believed to be eradicated (Table 5).

Table 5. Delacour's langur populations eradicated during the decade 2000-2010 (number and localities following Table 1).

No.	Locality	Survey	Last observation
10	Roc mountain	2008	before 2000
11	Phu Vinh mountainous area	2008	1999
12	Mai Chau mountainous area	2008	2002
15	Northern Ba Thuoc mountainous area	2008	before 2000
16	Ngoc Son mountainous area	2008	2004
17	Thiet Ong mountain	2006	before 2000
18	Nui Boi Yao mountainous area	2006	before 2000
19	Thach Thanh District	2010	before 2005

Distribution and Status of the species after 2010

Several surveys to monitor the development of populations were conducted after 2010. Only 9 areas are currently known where Delacour's langurs were recorded. It is from these areas that recent information and data were collected.

Survey organization and methods

A total of 20 surveys were carried out between 2012 to 2015 by the Endangered Primate Rescue Center (EPRC) and Forestry University Hanoi to verify the current situation of the species (Table 6).

Table 6. Surveys with the emphasis on Delacour's langur distribution and status after 2010.

No.	Locality	Survey Period	Organisation / Institution
1	Cuc Phuong National Park	January 2014 June 2015 July 2015	EPRC EPRC EPRC
2	Yen Mo mountain range	October 2014 February 2015	EPRC EPRC
3	Bim Son mountain range	June 2014 February 2015	EPRC EPRC
4	Hoa Lu Nature Reserve	June 2014 October / November 2014	EPRC EPRC
5, 6, 7	Van Long Nature Reserve	May 2014	EPRC
5, 6, 7	Van Long extension area	August 2012 August / September 2012 October / November 2012	EPRC EPRC EPRC
8	Kim Bang area,	November 2013 July 2014 October 2014	EPRC EPRC EPRC
9	Huong Son Cultural and Historical Site	March 2015	EPRC
13, 14	Pu Luong Nature Reserve	December 2011	University of Forestry

The surveys for this project were carried out by different survey teams, under leadership of Vietnamese biologists.

A survey team comprised mostly three to five people, the team leader, one or two forest rangers and one to two local villagers who are familiar with the area. The forest rangers consisted of staff from the protected area or if the area is not protected, staff of the district forest department. Larger areas or areas with difficult access were surveyed by two teams.

The duration of the surveys lasted from 5-17 days, depending on topography, and access to the area, and weather conditions.

Each field survey started with interviews of local people in order to gather information about date and localities of sightings. Locals are often very familiar with the area due to exploitation of several forest products, or even hunting and trapping. The Delacour's langurs are very well known by locals and with their unique appearance cannot be confused with other primate species in the area.

It is a useful practice to survey an area several times to evaluate and confirm the gathered information. Primate feces, collected from sleeping sites or in the surveyed areas were stored and identified by molecular genetic testing. The genetic identification was carried out by the German Primate Center.

Results of the surveys in the subpopulations

The results of the surveys in all known subpopulations shows a dramatic decline compared to the last decade (Table 1, 7 and 8). The total number is estimated at 234-275 individuals. The majority

occurs in Van Long Nature Reserve and if the population of the nature reserve is combined with the adjacent planned extension area to count as one population, the total for the area is 164-191 individuals. The remaining 70-84 individuals occur in the additional 7 areas (Table 7). Not one of these populations has a size which can guarantee a secure future, even if hunting could be eliminated. The problem of inbreeding for these small populations is not relevant. Before the inbreeding coefficient increases over a certain level, the populations will be extinct through other pressures.

Table 7. Overview about recorded groups and individuals of Delacour's langur in each subpopulation after 2010.

No.	Locality	Groups / Individuals confirmed	Groups / Individuals Interview	TOTAL Groups / Individuals estimated
1	Cuc Phuong National Park	2 / 3-4	1 / 7-9	2 / 10 - 13
2	Yen Mo mountain range	/	2? / > 10?	2? / < 10?
3	Bim Son mountain range	1 / 3?	3-4 / ?	3? / < 10?
4	Hoa Lu Nature Reserve	/	1 / 3-5	1 / 3-5
5, 6, 7	Van Long Nature Reserve	16-19 / 130-140	/	16-19 / 130-140
5, 6, 7	Van Long extension area	5 / ?	6 / 34-51	6 / 34-51
8	Kim Bang area	1 / 4-6	7 / 24-32	7 / 24-32
9	Huong Son Cultural and Historical Site	/	1 / 3-4	1 / 3-4
13, 14	Pu Luong Nature Reserve	/	? / 10	? / 10
	TOTAL	25-29 / 140-153	21 / 91- 121	37 / 234 - 275

Table 8. Classification and numbers of individuals in subpopulations after 2010.

Number of individuals in one subpopulation	1-10	11-20	21-30	> 40
Number of subpopulations	5	1	1	2
Number of individuals in these subpopulations	36-39	10-13	24-32	164-191
Percent of individuals of the total population in these subpopulations	~15%	~5%	~10%	~70%

The gathered data, despite all possible inaccuracy, show clearly the problem for the species and the extreme value of Van Long Nature Reserve as the last and only refuge which can enable the survival of the species.

Status of Delacour's langur in captivity

There exists only one small captive population of Delacour's langurs, which are housed at the EPRC. The goal of the EPRC is it to provide housing for confiscated individuals of highly endangered primate species, which should support the activities of forest rangers in law enforcement. These confiscated animals should act as founders for the establishment of small and stable captive populations and as a source for reintroduction if safe and adequate habitats are available.

The breeding program for Delacour's langur started with five wild caught, confiscated individuals. In 1996 the first animal ever of this species was born in captivity. In total, 23 individuals have been born at the EPRC, and currently the EPRC keeps 15 individuals. The reproduction rate of the species

is low with one individual been born on average, every two years per female. But the successful breeding program could provide stock for the establishment of a population in an adequately protected habitat.

Conservation interventions

Evidence of the dramatic decrease in populations was recognized and documented as long as 20 years ago. Conservation actions were provided and recommendations made to preserve this species. Unfortunately these early recommendations were never recognized and largely ignored (Do Thi Nga, 2013; Ebenau et al. 2011; Nadler et al. 2003; Nadler 2004). Beside the obviously stable and increasing population in Van Long Nature Reserve – based on special conditions – it is now foreseeable that no other population will have a chance for long-term survival. The current overview should be a wake up call and a starting point for actions.

Improvement of Protection

The primary focus of conservation activities for the species should be the protection of all remaining populations. But this is far from the reality. The protection of areas without current protection status - which are three areas (2, 3, 8) - is not feasible. To apply for a protection status and establish strong protection for an area is not a viable option for such extremely small populations with little chance of ever developing into viable populations. These populations will be eradicated and disappear in the near future.

The protection in protected areas – except Van Long Nature Reserve – is extremely low. The development of the population in Van Long - and similar examples in China for the white-headed langur (*Trachypithecus leucocephalus*) (Wenzshong Ran, 2003) and Francois langur (*Trachypithecus francoisi*) (Mingjing Li, 2004) - show a rapid increase of the population if hunting is eliminated. This means that a seemingly stable population in an intact habitat must be under hunting pressure, otherwise it would increase. But the populations in protected areas show a dramatic decrease as well – a sign of intensive poaching.

The relatively low protection in the protected areas is not solely based on low protection activities of the ranger staff, but also the difficult topography and accessibility of the areas hindering effective protection work, e.g. the long and narrow area of Cuc Phuong National Park provides a very long border and easy access to the core areas.

An immediate and drastic improvement of protection for the protected areas is no longer a realistic option for supporting the development of viable populations, as even with protection, the populations are now too small to ever be viable.

Habitat extension

The most efficient option to stabilize the largest existing population and to save sufficient habitat for the long-term existence of a viable population would be the extension of Van Long Nature Reserve. The possible extension area is about 4000 ha and therefore larger than the existing nature reserve, has similar habitat structure and forest cover. There are still no settlements in the appointed area. The total area would be more than 7000 ha. This would be the size which enables also the upgrade of the nature reserve to national park status. As a national park the area will receive much higher national and international attention, higher financial support and a higher number of staff.

Despite intensive efforts over several years the process is extremely slow and there is yet no obvious progression towards success. Three provincial Forest Protection Departments, Ninh Binh Province for the existing Van Long Nature Reserve, Hoa Binh Province for the possible extension area and Ha Nam Province as the province adjacent to the provincial border, have already signed an agreement and statement about the extension, but till now the Ninh Binh provincial administration (DARD) has refused the application for an extension.

The extension of Van Long Nature Reserve in the direction of the Kim Bang area, at least partly, and with the establishment of a corridor could also be of high benefit to the population and support the exchange of individuals. But the designation of the Kim Bang area for industrial exploitation for the cement industry and future tourism development make such option not feasible.

Translocation

Translocation of isolated groups of animals or small populations from areas under pressure or for improving the genetic pool of a larger population is undoubtedly for many species an important tool for conservation. Fragmentation of populations is an increasing problem. The surveys during the project time were carried out with an emphasis to assess the conditions of smaller populations for translocation actions. The most critical point is the method with which to catch the animals in the areas with often very difficult access. One way is netting of the animals in a cave, a sleeping place which the animals occasionally or preferentially use in the winter season. Special caves and cracks in the limestone outcrops are often used consistently by generations of animals in one group. But groups which use easily accessible caves are as a consequence of easy access, already wiped out by hunters and the remaining sleeping places are very difficult to access.

Currently there is no other proven technique for capturing animals in the difficult terrain that constitutes their natural habitat.

A high personal, financial and technical expenditure would be necessary to develop a technique to safely capture animals in the wild.

Reintroduction

A basis for reintroduction is the captive population of Delacour's langur at the Endangered Primate Rescue Center. In 2011 a first pilot project was conducted with the reintroduction of three captive born individuals into Van Long Nature Reserve (Agmen, 2014; Beaumont, 2012; Nadler 2012). Based on the successful result a second reintroduction took place in November 2012, also in Van Long Nature Reserve (Elser 2014; Elser et al., 2015). The programs have been very positively received by villagers and the awareness about protection of the species in the communes surrounding the nature reserve is very high. This has resulted in the long-term success of the Frankfurt Zoological Society conservation project and the strong involvement of local villagers and guards of the community protection unit in protection and conservation activities (Elser et al., 2013).

Based on the current status of the subpopulations at other sites and the low level of protection existing for them, the only viable option is to reintroduce captive bred individuals into Van Long Nature Reserve or to establish another new population in a well protected area.

From a conservation point of view, the establishment of a second population would be a preferable option in order to

secure the long-term existence of the species. With a search of possible areas, only the newly nominated World Heritage Site "Trang An Scenic Landscape Complex" could provide a suitable habitat for a newly established population (Fig. 3). This 6000 ha area comprises larger limestone blocks surrounded by water and several islands (Fig. 4).



Fig.3. The limestone area with the World Heritage Site "Trang An Scenic Landscape Complex" including Hoa Lu Nature Reserve.



Fig.4. Islands in the World Heritage Site “Trang An Scenic Landscape Complex” which could serve as habitat for single groups of Delacour’s langurs. Island 1 ca. 1.5 ha; Island 2 ca. 1.5 ha; Island 3 ca. 6 ha; Island 4 ca. 5 ha.

As a first step small groups could be released to islands for ease of monitoring and management, including, animal exchange or removal of animals to other areas. With a growing number of individuals the release of animals from the islands into the larger area to establish a larger population could be feasible.

The area is a tourism spot and the langurs on the islands would not be disturbed by tourist boats provided entry to the islands was prohibited. Similar to Van Long Nature Reserve the animals on the limestone cliffs can be easily observed. This could be also widely used for education purposes and to spread the message about the dramatic situation for the species. For the area it would also be an interesting and additional highlight for tourists. This reintroduction project will be supported by the provincial Forest Protection Department Ninh Binh.

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The skeletal anatomy of the douc langurs (Genus *Pygathrix*)

Craig D. Byron, Cassandra Hensel, Jarred Morrison and Hoang Nguyen

Mercer University, Department of Biology, 1501 Mercer University Drive, Macon, GA 31207.

Corresponding author: Craig Byron <byron_cd@mercer.edu>

Key words: Douc langur, odd-nosed colobine, *Pygathrix*, skeletal data

Summary

The odd-nosed genus *Pygathrix* of Southeast Asia has been understudied in the history of primate functional morphology because they are endemic to less documented geographical regions, fragile in captivity, and rare in museum collections. This study presents a description of morphological variables in male and female *Pygathrix* langurs throughout the axial and appendicular skeleton that are known to convey information about an individual's size and potential locomotor mode. The sample includes *P. cinerea*, *P. nemaus*, and *P. nigripes* from the Field Museum of Natural History, Chicago, the Museum of Comparative Zoology, Cambridge, Muséum National d'Histoire Naturelle, Paris, and the Endangered Primate Rescue Center, Cuc Phuong National Park, Vietnam.

Four linear metrics showed sexual dimorphism in the wrist, elbow, knee, and crus of the leg with males being significantly larger. Additionally, two key ratiometric indices, the intermembral index and the brachial index, show values that are intermediate between those of brachiators and more typical arboreal quadrupeds. Sexual dimorphism in load bearing regions of the arms and legs is expected of catarrhine primates. In brachiators such load bearing regions are concentrated in the forelimb while in more quadrupedal taxa they are dispersed between fore- and hindlimbs, or found mostly in the hindlimb. For both the linear metrics and the ratiometric index data this pattern of contrasts is consistent with the notion that the douc genus is a compelling example of an Old-World semibrachiator. It is hoped that these data can inform studies of ape evolution and the pronograde to orthograde transition.

Nghiên cứu giải phẫu học về xương ở những loài vọc chà vá (giống *Pygathrix*)

Tóm tắt

Những nghiên cứu về hình thái chức năng xương loài vọc thuộc giống *Pygathrix* ở khu vực Đông Nam Á còn hạn chế. Bởi vì mẫu vật trong bảo tàng ít và những cá thể nuôi nhốt phân tán. Đặc điểm hình thái của xương chi, thân và hộp sọ của giống *Pygathrix* được phân tích trong nghiên cứu này. Những số đo hình thái phản ánh kích thước cơ thể và liên quan đến cách di chuyển của loài. Mẫu bao gồm ba loài, chà vá chân xám, chà vá chân nâu, và chà vá chân đen. Mẫu thuộc bảo tàng lịch sử tự nhiên Chicago, bảo tàng động vật Cambridge, bảo tàng lịch sử tự nhiên Paris, và Trung tâm Cứu hộ Linh trưởng Nguy cấp, Ninh Bình, Việt Nam. Kết quả cho thấy có sự sai khác đáng kể 4 số đo hình thái xương giữa con đực và con cái. Các số đo về độ dài, rộng của xương cổ tay, xương cẳng tay, xương đầu gối, và xương cẳng chân ở con đực lớn hơn ở con cái. Hai chỉ số intermembral và brachial đã được phân tích cho thấy giống chà vá vừa có kiểu di chuyển chuyên cành bằng chi trước vừa có đặc trưng của kiểu di chuyển bằng bốn chi trên cây. Sự khác biệt các chỉ số đo xương chân và tay giữa hai giới tính phù hợp với nhóm linh trưởng Khỉ mũi hẹp.

Ở những loài có kiểu di chuyển chuyên cành vùng xương chịu lực tập trung ở những chi trước, trong khi đó ở những loài di chuyển bằng bốn chân, lực phân tán lên xương ở cả chi trước và chi sau, nhưng tập trung ở các sau. Những số đo và các chỉ số hình thái xương của giống chà vá phản ánh kiểu di chuyển nửa chuyên cành đặc trưng ở Khỉ cụ lực địa. Những số liệu này là cơ sở để nghiên cứu về sự tiến hóa trong kiểu di chuyển ở những loài vượn, từ đi bằng bốn chân đến đi thẳng bằng hai chân.

Introduction

Odd-nosed colobines, comprised of the genera *Rhinopithecus*, *Pygathrix*, *Nasalis*, and *Simias*, form a monophyletic clade and are found in habitats throughout East and Southeast Asia (Liedigk et al., 2012). Many of these taxa display striking facial coloration and body pelage patterns as well as a larger body size when compared to other Asian colobines (Disotell, 1998; Jablonski & Ru-Liang, 1995; Jablonski & Zhang, 1992). With habitat loss and high levels of human predation pressure, the population outlook for this group remains threatened (Lippold & Thanh, 1998; Long, 2004; Nadler & Streicher, 2004; Nadler et al., 2003). As an example, the grey-shanked douc langur (*Pygathrix cinerea*) has been listed as a top-25 critically endangered primate on the IUCN's Red List (www.iucnredlist.org) since its inception. Thus, documenting the skeletal anatomy and positional behavior of such critically endangered taxa is a priority for primate functional morphologists. Aside from descriptions of *Nasalis*, there are very few morphological studies of odd-nosed colobines, in part, because they are not well represented in natural history museum collections, are endemic to less documented geographical regions, and can be fragile in captivity (Lippold, 1998; Nadler et al., 2003; Sterling et al., 2006). In an effort to provide additional morphological data for this group, we describe here a sample of the genus *Pygathrix*: *P. nemaus*, *P. cinerea*, and *P. nigripes*.

Primate skeletal anatomy is of interest insofar as correlations between morphology and functional attributes like dietary and/or locomotor behavior are well established in the literature (Shea, 2005). These correlations allow predictions to be made concerning living and extinct taxa and their adaptive niche based on skeletal morphometrics. Historically, primate limb anatomy studied as a demonstration in adaptive diversity, with a plethora of studies that developed a classificatory scheme based on these morphological data (Ashton & Oxnard, 1964; Avis, 1962; Gregory, 1928; Larson, 1993; 1995; Napier, 1963; 1967; Napier & Napier, 1967; Oxnard, 1963; Schultz, 1930). A basic version of this scheme, as presented by Napier & Napier (1967), includes vertical clinging and leaping, quadrupedalism, brachiation, and bipedalism. With the exception of quadrupedalism, these locomotor categories represent relatively specialized modes that are independent of each other and occupy extreme positions derived from more primitive and generalized locomotor behaviors in smaller bodied primate ancestors. Quadrupedalism is central to this and likely represents the antecedent condition to other more specialized non-quadrupedal modes included in this scheme. However, quadrupedalism is also an all-encompassing category that overlaps with, or transitions into, the other categories, including brachiation and the transitional semibrachiation.

As a category in itself, semibrachiation, defined as the reliance on quadrupedal and forelimb dominated suspensory postures, has been problematic because it is expressed differently in New World platyrrhine monkeys as compared to Old World catarrhine monkeys. The New World semibrachiators are represented by the various genera of the prehensile tailed family Atelidae and are more specialized when compared to smaller platyrrhine monkeys with more generalized and primitive arboreal modes (Jones, 2008; Rosenberger et al., 2008). New-World semibrachiators utilize a unique form of semibrachiation in which orthograde suspensory behavior is accompanied by pendular swinging behavior whereby the forelimbs and the tail grasp arboreal substrates (Schmitt et al., 2005; Turnquist et al., 1999). In contrast, the Old-World semibrachiator group is limited to exclusively forelimb-mediated suspensory behavior. The genera included in this scheme are *Nasalis*, *Rhinopithecus*, *Presbytis*, *Colobus*, and *Pygathrix* (Ashton & Oxnard, 1964; Napier, 1963; Napier & Napier, 1967).

Other variations on transitional categories of brachiation include those modes that precede modified or true brachiation as expressed in living apes. Unfortunately, there is not a living example of what this pre-ape locomotor behavior might look like. Taking a closer look at the Old World semibrachiator group represents an intriguing antecedent condition for the types of arm swinging locomotion found in stem hominoids. The genus *Pygathrix* makes a compelling model for this investigation. For ecological reasons, one can suggest that *Nasalis* and *Rhinopithecus* have a more derived habitat relative to a truly forest living arboreal catarrhine and thus are not suitable. These large-bodied genera are found in mangrove settings or at higher altitude and colder climate where a component of locomotion is terrestrial (Boonratana, 1993; Kawabe & Mano, 1972; Ruhayat, 1986; Zhu et al., 2014). Likewise *Presbytis* and *Trachypithecus* are not good candidates in differing from the other genera with body sizes that are smaller and locomotor behavior that is characterized by above-branch quadrupedalism with leaping

and climbing (Fleagle, 1976; 1977; 1978). Finally, the African leaf-monkey genus *Colobus* does not engage in a significant amount of suspensory behavior (Mittermeier & Fleagle, 1976; Morbeck, 1977; 1979; Struhsaker, 1975) and thus cannot serve as a model.

Since 2004 the literature on *Pygathrix* has shown that various species of this genus exhibit a significant amount of suspensory behavior, using an orthograde trunk, extended elbows, and the brachial aspect of the arm abducted above the head (Byron & Covert, 2004; Stevens et al., 2008; Workman & Covert, 2005; Wright et al., 2008). Thus, this taxon represents an ideal candidate to investigate for transitional morphological characters between orthograde apes and smaller sized, pronograde quadrupedal monkeys. This paper represents the first report on the basic skeletal morphology of a sizable sample of adult male and female douc monkeys. The sample detailed below includes red-, grey-, and black-shanked doucs (*P. nemaesus*, *P. cinerea* and *P. nigripes*) from the Endangered Primate Rescue Center (EPRC) in Cuc Phuong National Park, Vietnam. The animals were raised either in the wild or within the habitat appropriate housing found at the EPRC, and thus have engaged in natural types of semibrachiation. It is hoped that these reported data can help inform our understanding of early hominoid evolution and the pronograde to orthograde transition.

Materials and Methods

The total sample of monkeys used in this study includes 15 mature females, 21 mature males, and four of mature but undetermined sex, totaling 40 individuals. Twelve females and 19 males belong to three species, *P. cinerea*, *P. nemaesus*, and *P. nigripes*. There are five additional doucs in the sample that are one hybrid between *P. nemaesus* and *P. nigripes* and four of undetermined species taxonomy (Table 1). With the presumption that significant species level differences are absent, and in the interest of bolstering sample size, all are included in one sample for male and female doucs and tests of homogeneity are conducted. The sample is dominated by members of the EPRC populations either born in captivity or confiscated from the illegal trade in animals. However, a few specimens are represented by mostly incomplete skeletal materials found in the Field Museum of Natural History (Chicago, IL), Museum of Comparative Zoology (Cambridge, MA), and Muséum National d'Histoire Naturelle (Paris, France).

Table 1. Total of samples.

Species	female	male	sex unknown
<i>Pygathrix cinerea</i>	4	6	0
hybrid <i>P. nemaesus</i> x <i>P. nigripes</i>	0	1	0
<i>Pygathrix nemaesus</i>	7	9	4
<i>Pygathrix nigripes</i>	1	4	0
<i>Pygathrix</i> spp.	3	1	0
Total (n=40)	15	21	4

Morphometric data were collected using a pair of Mitutoyo digital hand calipers connected to a Macbook workstation running Microsoft Excel. Length in mm was recorded between anatomical landmarks to the nearest 0.01 mm. A total of sixty linear morphometrics were collected for the genus *Pygathrix* (Table 2). Several of the measurements were used to compute ten ratiometric index variables that quantify size and shape within specific anatomical compartments across the skeletal sample. Statistical analysis was carried out using JMP Pro 11 software (SAS) to derive standard descriptive statistics as well as the Shapiro-Wilk W test for goodness of fit. In cases where significant W statistics were observed, further t-tests were conducted that compared female and male groups. Landmarks for these variables are considered standard for anyone familiar with skeletal anatomy and so will not be described in further detail except where necessary.

Table 2. Descriptive statistics for adult douc langurs (Genus *Pygathrix*).

Differences Between Sexes = Significant Shapiro-Wilk (W) Statistic as a Goodness-of-Fit Test
All linear measurements are reported to the nearest 0.01 mm. Ratios are presented as %.

Dependent Variable	<i>Pygathrix</i> (male or female)	n =	μ	\pm	σ	W-Stat	P-Value
Scapular Height (mm)	female	13	69.86	6.07		0.859	P<0.05
	male	18	76.19	5.11		0.953	NS
	Total Sample	35	73.05	7		0.946	NS
Scapular Height (mm)	female	15	55.15	4.532		0.966	NS
	male	19	63.86	5.229		0.960	NS
	Total Sample	38	59.84	6.612		0.973	NS
Glenoid Height (mm)	female	13	17.31	1.522		0.959	NS
	male	18	19.54	1.067		0.946	NS
	Total Sample	35	18.59	1.779		0.961	NS
Glenoid Width (mm)	female	13	11.99	1.317		0.808	P<0.01
	male	18	13.58	1.016		0.980	NS
	Total Sample	35	12.88	1.383		0.972	NS
Clavicle Length (mm)	female	12	59.11	4.771		0.911	NS
	male	17	67.61	5.38		0.964	NS
	Total Sample	33	63.78	6.66		0.985	NS
Humerus Length (mm)	female	15	179.3	13.85		0.913	NS
	male	20	195.9	10.24		0.980	NS
	Total Sample	38	188.6	15.6		0.968	NS
Humerus Midshaft Circumference (mm)	female	15	32.33	3.222		0.956	NS
	male	20	35.65	2.621		0.907	NS
	Total Sample	38	34.32	3.519		0.966	NS
Humerus Midshaft Breadth (mm)	female	12	9.866	1.033		0.939	NS
	male	17	10.72	0.7482		0.976	NS
	Total Sample	32	10.3	1.039		0.951	NS
Humerus Midshaft Depth (mm)	female	12	10.09	0.7572		0.965	NS
	male	17	11.11	1.025		0.957	NS
	Total Sample	32	10.64	1.169		0.982	NS
Humerus Head Height (mm)	female	12	18.29	1.89		0.947	NS
	male	17	20.2	1.131		0.971	NS
	Total Sample	32	19.2	1.906		0.935	NS
Humerus Head Width (mm)	female	12	16.73	1.199		0.958	NS
	male	17	18.92	1.181		0.977	NS
	Total Sample	32	17.89	1.646		0.980	NS
Humerus Biepicondylar Width (mm)	female	12	27.21	2.41		0.894	NS
	male	17	31.67	2.034		0.940	NS
	Total Sample	32	29.74	3.179		0.953	NS
Capitulum Width (mm)	female	12	9.461	1.002		0.939	NS
	male	16	10.36	0.7306		0.969	NS
	Total Sample	31	9.938	0.9785		0.979	NS
Trochlear Width (mm)	female	12	10.8	1.04		0.955	NS
	male	16	12.08	1.102		0.930	NS
	Total Sample	31	11.46	1.259		0.972	NS

Ulna Length (mm)	female	11	199.01	16.67	0.880	NS
	male	16	224.5	10.77	0.928	NS
	Total Sample	32	213.52	19.85	0.958	NS
Ulna Midshaft Circumference (mm)	female	11	20.18	3.12	0.903	NS
	male	16	22.81	2.64	0.963	NS
	Total Sample	32	21.91	3.04	0.953	NS
Ulna Midshaft Breadth (mm)	female	11	5.01	0.89	0.917	NS
	male	16	5.75	0.675	0.969	NS
	Total Sample	32	5.4	0.844	0.970	NS
Ulna Midshaft Depth (mm)	female	11	6.94	1.18	0.945	NS
	male	16	7.99	1.22	0.948	NS
	Total Sample	32	7.55	1.233	0.985	NS
Semilunar Notch Height (mm)	female	11	7.91	0.89	0.946	NS
	male	16	8.4	0.65	0.930	NS
	Total Sample	32	9.36	2.85	0.699	P<0.001
Olecranon Process Length (mm)	female	12	7.679	1.663	0.868	NS
	male	17	8.347	1.021	0.901	NS
	Total Sample	32	8.168	1.347	0.956	NS
Ulna Distal Condyle Width (mm)	female	11	7.66	1.04	0.927	NS
	male	16	8.94	1.09	0.852	P<0.05
	Total Sample	32	8.51	1.3	0.947	NS
Radius Length (mm)	female	11	8.17	0.77	0.949	NS
	male	16	9.79	0.69	0.857	P<0.05
	Total Sample	32	9.01	1.12	0.957	NS
Radius Midshaft Circumference (mm)	female	11	185.3	18.43	0.930	NS
	male	16	209.56	10.57	0.965	NS
	Total Sample	32	198.7	19.94	0.941	NS
Radius Midshaft Breadth (mm)	female	11	22.64	3.2	0.907	NS
	male	16	25.56	2.42	0.953	NS
	Total Sample	32	24.38	3.63	0.974	NS
Radius Midshaft Depth (mm)	female	11	7.32	1.25	0.945	NS
	male	16	8.09	0.73	0.935	NS
	Total Sample	32	7.69	1.04	0.950	NS
Radial Head Maximum Diameter (mm)	female	11	6.41	0.86	0.944	NS
	male	16	7.47	0.99	0.940	NS
	Total Sample	32	7.05	1.09	0.977	NS
Radial Head Minimum Diameter (mm)	female	11	14.07	1.37	0.941	NS
	male	16	16.13	0.72	0.941	NS
	Total Sample	32	15.16	1.53	0.905	P<0.01
Radial Head Circumference (mm)	female	11	12.07	1.13	0.968	NS
	male	16	13.83	0.78	0.965	NS
	Total Sample	32	13.03	1.32	0.945	NS
Radial Neck Circumference (mm)	female	11	41.91	4.16	0.951	NS
	male	16	47.13	2.58	0.959	NS
	Total Sample	32	44.66	4.69	0.931	P<0.05
Cervical Region Length (mm)	female	11	25	3.46	0.931	NS
	male	16	27.38	2.42	0.888	NS
	Total Sample	32	26.34	3.5	0.945	NS

Thoracic Region Length (mm)	female	10	129.42	11.99	0.874	NS
	male	16	134.55	28.83	0.857	P<0.05
	Total Sample	26	132.58	23.61	0.892	P<0.05
Lumbar Region Length (mm)	female	10	146.97	16.97	0.836	P<0.05
	male	17	149.67	29.96	0.880	P<0.05
	Total Sample	27	148.67	25.67	0.904	P<0.05
Sacrum Length (mm)	female	9	41.21	4.79	0.888	NS
	male	17	41.57	6.35	0.956	NS
	Total Sample	26	41.45	5.76	0.945	NS
Pelvis Height (mm)	female	12	136.17	9.3	0.919	NS
	male	17	147.14	8.24	0.939	NS
	Total Sample	32	141.86	10.93	0.972	NS
Ilium Length (mm)	female	12	86.22	7.45	0.897	NS
	male	17	89.6	5.37	0.959	NS
	Total Sample	32	88.1	6.68	0.977	NS
Ilium Breadth (mm)	female	12	35.94	3.31	0.904	NS
	male	17	39.97	3.92	0.970	NS
	Total Sample	32	37.99	4.2	0.966	NS
Ischium Length (mm)	female	12	24.95	4.03	0.823	P<0.05
	male	17	28.1	3.84	0.888	P<0.05
	Total Sample	32	27.46	4.56	0.934	NS
Pubis Length (mm)	female	12	38.03	3.9	0.973	NS
	male	17	38.1	3.29	0.893	NS
	Total Sample	32	38.33	3.73	0.947	NS
Acetabulum Height (mm)	female	12	21.61	1.84	0.972	NS
	male	17	22.98	1.28	0.968	NS
	Total Sample	32	22.37	1.69	0.979	NS
Acetabulum Width (mm)	female	12	17.45	1.89	0.919	NS
	male	17	18.55	1.55	0.948	NS
	Total Sample	32	18.08	1.72	0.989	NS
Femur Length (mm)	female	11	210.7	14.45	0.890	NS
	male	17	230.4	9.823	0.946	NS
	Total Sample	31	221.62	16.56	0.945	NS
Femur Midshaft Circumference (mm)	female	11	37.36	4.202	0.944	NS
	male	17	40.24	2.84	0.895	NS
	Total Sample	31	39.23	3.766	0.948	NS
Femur Midshaft Breadth (mm)	female	11	11.71	1.407	0.971	NS
	male	17	12.54	1.161	0.948	NS
	Total Sample	31	12.15	1.379	0.951	NS
Femur Midshaft Depth (mm)	female	11	11.23	1.124	0.968	NS
	male	17	12.37	0.87	0.975	NS
	Total Sample	31	11.87	1.146	0.964	NS
Femur Head Height (mm)	female	11	17.17	1.402	0.890	NS
	male	17	18.77	0.8895	0.960	NS
	Total Sample	31	18.02	1.387	0.957	NS
Femur Head Width (mm)	female	11	17.06	1.332	0.887	NS
	male	17	18.77	0.7935	0.966	NS
	Total Sample	31	17.98	1.357	0.952	NS

Femur Biepicondylar Width (mm)	female	11	28.3	2.324	0.945	NS
	male	17	31.96	1.407	0.930	NS
	Total Sample	31	30.47	2.556	0.947	NS
Femur Condyle Depth (mm)	female	11	23.69	1.738	0.920	NS
	male	17	26.58	1.166	0.964	NS
	Total Sample	31	25.37	2.105	0.934	NS
Tibia Length (mm)	female	11	187.94	12.37	0.927	NS
	male	16	207.27	9.65	0.967	NS
	Total Sample	32	199.05	15.41	0.969	NS
Tibia Midshaft Circumference (mm)	female	11	36.18	4.62	0.895	NS
	male	16	40	3.52	0.924	NS
	Total Sample	32	38.66	4.55	0.905	P<0.01
Tibia Midshaft Breadth (mm)	female	11	8.59	1.34	0.967	NS
	male	16	9.46	1.02	0.956	NS
	Total Sample	32	9.14	1.2	0.984	NS
Tibia Midshaft Depth (mm)	female	11	13.21	1.79	0.908	NS
	male	16	14.63	1.08	0.942	NS
	Total Sample	32	14.01	1.66	0.940	NS
Tibia Plateau Breadth (mm)	female	11	26.78	3.13	0.930	NS
	male	16	30.39	3.13	0.750	P<0.001
	Total Sample	32	29.13	3.48	0.917	P<0.05
Tibia Plateau Depth (mm)	female	11	20.99	3.24	0.889	NS
	male	16	22.87	2.7	0.918	NS
	Total Sample	32	22.22	3.09	0.961	NS
Tibia Distal Width (mm)	female	11	18.15	1.73	0.969	NS
	male	16	20.53	1.23	0.954	NS
	Total Sample	32	19.57	1.79	0.976	NS
Tibia Distal Depth (mm)	female	11	14.83	1.05	0.896	NS
	male	16	17.08	1.2	0.908	NS
	Total Sample	32	16.24	1.52	0.970	NS
Fibula Length (mm)	female	11	172.31	10.22	0.962	NS
	male	16	190.89	10.82	0.915	NS
	Total Sample	31	182.94	15.76	0.985	NS
Calcaneus Length (mm)	female	11	34.9	2.29	0.895	NS
	male	16	38.98	2.28	0.937	NS
	Total Sample	31	37.24	3.03	0.945	NS
Talus Length (mm)	female	11	23.78	1.38	0.931	NS
	male	16	27.19	1.33	0.907	NS
	Total Sample	30	26	2.28	0.970	NS
Talus Trochlear Breadth (mm)	female	11	12.35	1.03	0.959	NS
	male	16	13.94	0.95	0.978	NS
	Total Sample	30	13.27	1.23	0.978	NS
Intermembral Index (%)	female	11	91.18	5.755	0.863	NS
	male	16	93.11	1.752	0.952	NS
	Total Sample	30	92.37	3.9	0.834	P<0.001
Brachial Index (%)	female	12	103.5	4.979	0.913	NS
	male	16	106.2	3.217	0.941	NS
	Total Sample	31	104.7	4.25	0.923	P<0.05

Crural Index (%)	female	11	89.2	1.49	0.928	NS
	male	16	90.17	1.464	0.961	NS
	Total Sample	30	89.77	1.509	0.959	NS
Scapular Shape Index (%) Height / Width	female	12	125.84	10.16	0.9214	NS
	male	17	118.46	8.89	0.9407	NS
	Total Sample	35	121.32	9.38	0.9494	NS
Clavicle Index (%) Clavicle Length / ((Acetabulum Height*Width) ^{1/2})	female	12	305.3	17.91	0.900	NS
	male	17	329.1	35.44	0.953	NS
	Total Sample	32	317.7	31.08	0.954	NS
Humerus Gracility Index (%) Humerus Length / ((circumference* breadth*depth) ^{1/3})	female	12	1223	133.3	0.965	NS
	male	17	1227	76.7	0.944	NS
	Total Sample	32	1226	97.28	0.962	NS
Ulna Gracility Index (%) Ulna Length / ((circumference* breadth*depth) ^{1/3})	female	11	2297.25	411	0.9581	NS
	male	16	2239.59	256.23	0.9443	NS
	Total Sample	32	2252.48	296.97	0.9569	NS
Olecranon Length Index (%) Olecranon Process Length / ((Acetabulum Height*Width) ^{1/2})	female	11	40.18	6.43	0.9527	NS
	male	16	43.74	5.26	0.9514	NS
	Total Sample	31	42.06	5.62	0.9765	NS
Radius Gracility Index (%) Radius Length / ((circumference* breadth*depth) ^{1/3})	female	12	1832	259.6	0.976	NS
	male	17	1822	159.6	0.926	NS
	Total Sample	32	1832	197.1	0.981	NS
Lumbar Index (%) (Lumbar Height / Thoracic Height)	female	9	107.63	8.42	0.842	NS
	male	14	108.3	7.6	0.933	NS
	Total Sample	23	110.58	8.3	0.942	NS

Results

In total 60 variables from the post-cranial skeleton are reported from the largest known sample of the genus *Pygathrix*. Overall, they describe an arboreal, tailed, Old World monkey that is medium to large bodied. The computed *W*-statistic represents a test of homogeneity with the null hypothesis that one single distribution of data is observed and not something with multimodal and non-normal data. The closer the *W*-stat is to 1.0, the closer to complete uniformity in the data. Significant *p*-values indicate significantly low *W*-statistics and reject the null hypotheses (i.e., the distribution of that group for that dependent variable is not uniform and is therefore non-normal).

Significantly non-homogenous variables are Scapula Height, Glenoid Width, Semilunar Notch Height, Ulna Distal Condyle Width (UDCW), Radius Length, Radial Head Minimum Diameter, Radial Neck Circumference (RNC), Thoracic Region Length, Lumbar Region Length, Ischium Length, Tibia Midshaft Circumference (TMC), and Tibial Plateau Breadth (TPB). Of these variables RNC, UDCW, TMC, and TPB (of the elbow, wrist, knee and crus of the lower leg) are the only ones that exhibit significant sexual dimorphism revealed by *t*-tests comparing known male and female groups. Each of these four comparisons from the elbow, wrist, and the lower leg where males which are significantly larger than females (Fig. 1).

Additionally, two key ratiometric indices exhibit sexual dimorphism, the Intermembral Index (IM),

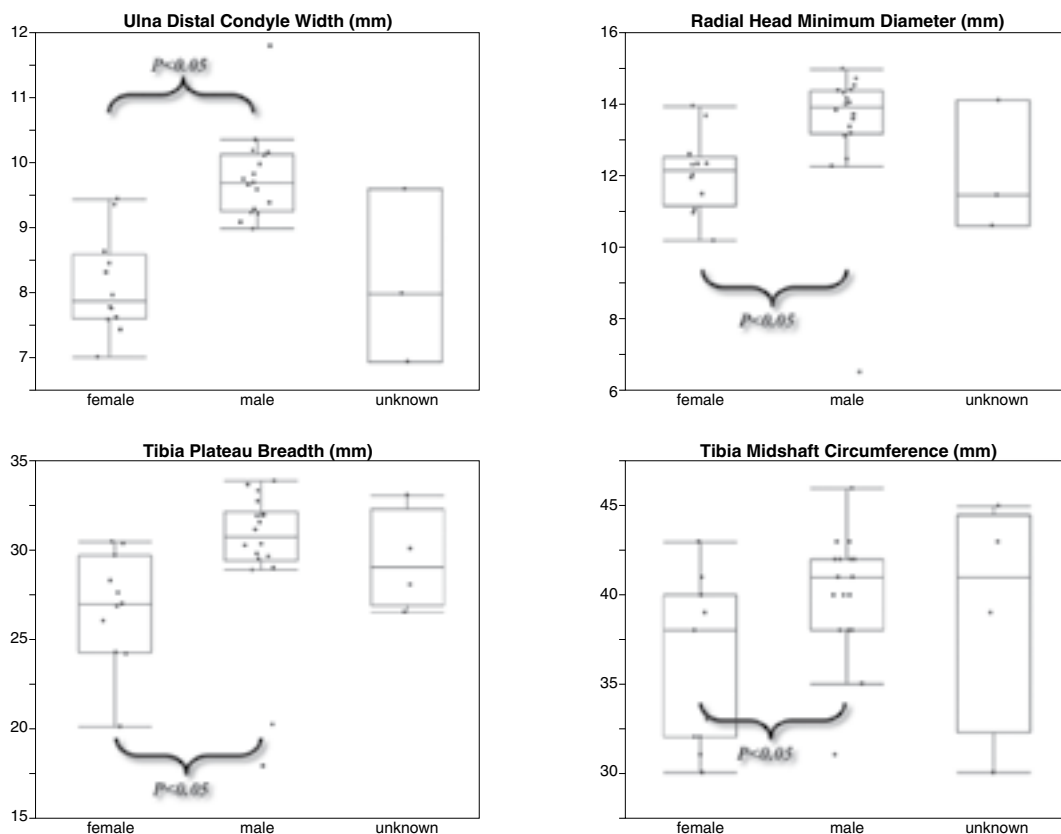


Fig.1. Four linear metrics that showed significant sexual dimorphism. Significant p-value represents a rejection of the null hypothesis that males and females are the same and uses a t-test. Unknowns were left out of the t-test.

and Brachial Index (BR). They show values that are intermediate between those of brachiators and more typical arboreal quadrupeds. As a total sample the IM was 92.4% with males showing slightly larger (93.1%) than female (91.2%) values. The BR for the total sample was 104.7% with males (106.2%) being larger than females (103.5%) in this measure. Thus, the douc langur has relatively long arms and forearms consistent with more suspensory locomotor habits. Furthermore, the larger male specimens are in an even greater direction toward suspensory morphology having relatively longer arms and forearms than even female doucs.

Discussion/Conclusions

In this study a sample of 40 adult douc langurs of the genus *Pygathrix* are described. A series of basic skeletal measurements derived from limb, girdle, and vertebral regions are presented. Four variables were observed to show significant sexual dimorphism at the elbow, wrist, knee, and the lower leg (Fig. 1). This sexual dimorphism is not surprising given that each feature is found at a major load-bearing region of the fore- and hindlimb. Increased tibial loadings would be true of larger sizes for quadrupedal locomotion. Increased forearm loadings would be true of larger sizes for forelimb mediated suspensory behavior. This pattern of significance underscores the transitional nature of the semibrachiator category and the importance of *Pygathrix* as a catarrhine representative.

In this study, the genus *Pygathrix* is described as a homogenous statistical population and so is not divided into species or sex. For the sake of comparative contrast with other catarrhines, this facilitates testing the morphological substantiation of the “Old-World Semibrachiator” category (Ashton & Oxnard, 1964; Napier, 1963). This test of the semibrachiator concept is relevant because of findings that many colobines from that earlier category do not arm swinging, and thus, are not

actually semibrachiators (Mittermeier & Fleagle, 1976; Morbeck, 1977; 1979). Recent attention has been paid to doucs because they do complement their quadrupedal locomotion with armswinging (Byron & Covert, 2004; Covert et al., 2004; Stevens et al., 2008; Wright et al., 2008) making them an ideal taxon to understand the evolutionary origins of orthograde positional behavior.

In the classic description of the Old-World semibrachiator group (Napier & Napier, 1967) reports of average intermembral index (93%) and brachial index (104%) are cited for *Pygathrix* from earlier work (Milne-Edwards & Pousargues, 1898; Washburn, 1942). Only one other odd-nosed Asian Colobine has such high values for these indices, the proboscis monkey, Genus: *Nasalis*. The other colobines of Asia and Africa have lower intermembral and brachial index values in the range of typical arboreal quadrupeds (i.e., the legs are relatively longer than arms and the antebrachium is relatively shorter than the brachium). In the most specialized brachiators like *Hylobates*, an intermembral index of 129% and brachial index of 113% are reported, indicating how forelimb (and forearm) dominated these animals are (Schultz, 1930). Among platyrrhines the New World semibrachiators more closely approximate the limb index condition of true brachiators. However, with a prehensile tail as a major component of the locomotor stride, this group does not exhibit a transitional condition that is relevant to the pronograde to orthograde transition that occurred in catarrhine primates.

The results for *Pygathrix* presented in this paper are intermediate between typical arboreal quadrupedal monkeys and true gibbon-type brachiators, and match expectations for this taxon. This douc sample's intermembral index is $92.4 \pm 3.9\%$ and the brachial index is $104.7 \pm 4.3\%$. These data are significant because they provide information on the skeletal anatomy of a medium-sized catarrhine leaf monkey that exhibits sexual dimorphism and is adapted for a highly arboreal habitat. For these reasons, *Pygathrix* is a compelling model for early hominoid evolution and the origins of orthograde suspensory behavior.

Having a transitional type of locomotor behavior that overlaps with true brachiators as well as quadrupedal catarrhines is also predicted for a group designated pro-brachiation that purportedly includes ancestral hominoid taxa like *Proconsul* (Napier, 1963). These taxa precede the true brachiation of more derived hominoids (like chimps and gibbons). Recent work on an extinct stem catarrhine taxa from the European Miocene describes functional similarities with New World semibrachiators that are interpreted to mean that *Pliopithecus vindobonensis* likely performed forelimb suspensory locomotion (Arias-Martorell et al., 2014; Rein et al., 2015). Most recently reports of a more modern stem hominoid from the European Miocene describe *Pliobates cataloniae* as an arboreal, small-bodied, quadruped with a wrist that permitted greater rotation (Alba et al., 2015; Benefit & McCrossin, 2015). Including *Pygathrix* in these types of analyses should be a goal for anyone interested in ape locomotion and evolution. Currently these types of analyses are standard for primate taxa commonly found in natural history museum collections. It is hoped that the results presented here, and the availability of the EPRC skeletal collection to future investigators, help inform more complete studies of primate morphology.

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Intrageneric shape variation of douc langur scapula (Genus *Pygathrix*)

Katie E. Bailey¹ and James D. Pampush²

¹ Texas A&M University, Department of Anthropology, Collage Station, TX

² Duke University, Department of Evolutionary Anthropology, Durham, NC
Corresponding author: Katie E. Bailey <katie__9808@tamu.edu>

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Summary

The genus *Pygathrix* consists of three species, the red-shanked douc langur (*Pygathrix neameus*), the grey-shanked douc langur (*P. cinerea*) and the black-shanked douc langur (*P. nigripes*). These primates are found in Southeast Asia in Laos PDR, Cambodia, and Vietnam, where they occur only east of the Mekong River. The Endangered Primate Rescue Center (EPRC) in Northern Vietnam has lent itself to comparative locomotor studies of the red-shanked and the grey-shanked douc langurs where both have been observed to regularly engage in brachiation and forelimb suspension. The grey-shanked douc langur was observed engaging in forelimb suspension approximately 56% of all locomotor bouts whereas the red-shanked douc langur used forelimb suspension about 46% of all locomotor bouts. Historical literature placed the doucs into the semibrachiator locomotor category but also suggested arm-swinging was infrequent.

Scapular shape plays a central role in the ability for a primate to engage in forelimb suspension and brachiation-type behaviors. We examined the scapular diversity within the genus *Pygathrix* to document morphological variation. We observe that the douc langurs share a similar scapular morphology and therefore - by extension - share a locomotor repertoire that includes suspensory behaviors. We used 17 3D landmarks to gather shape data on the scapula of the genus *Pygathrix*. Our results show no significant difference between the scapular shape of the three species ($P = 0.354$, $P = 0.344$). These results suggest *Pygathrix* is monomorphic for scapular shape.

Nghiên cứu về hình dạng xương bả vai giữa các loài voọc Chà vá (giống *Pygathrix*)

Tóm tắt

Giống *Pygathrix* có 3 loài gồm voọc Chà vá chân nâu (*Pygathrix nemaeus*), Chà vá chân xám (*P. cinerea*) và Chà vá chân đen (*P. nigripes*). Những loài này phân bố ở một số quốc gia vùng Đông Nam Á gồm Lào, Cambodia, và Việt Nam, phía đông của sông Mê Kông. Những nghiên cứu so sánh về sự vận động giữa hai loài Chà vá chân nâu và Chà vá chân xám đã được thực hiện tại Trung tâm Cứu hộ Linh trưởng nguy cấp. Kết quả cho thấy cả hai loài đều có kiểu di chuyển chuyên cành và treo người bằng hai chi trước.

Cụ thể, kiểu di chuyển treo người trên hai chi trước chiếm 56% ở loài Chà vá chân xám có và 46% ở loài Chà vá chân nâu. Các tài liệu trước đây cũng khẳng định các loài chà vá có kiểu di chuyển bán chuyên cành và không thường xuyên di chuyển theo kiểu tung người và bám bằng hai chi trước.

Nghiên cứu về hình dạng của xương bả vai có vai trò quan trọng trong việc tìm hiểu khả năng di chuyển chuyên cành và tung người. Chúng tôi đã phân tích các số đo và chỉ số liên quan để thấy được sự đa dạng về hình thái của xương bả vai giữa các loài chà vá. Chúng tôi thấy rằng hình thái xương bả vai của các loài chà vá về cơ bản giống nhau, do đó có cũng những kiểu di chuyển bao gồm cả kiểu vận động treo người. Chúng tôi đã phân tích 17 số đo 3 chiều của xương bả vai của các loài chà vá. Kết quả cho thấy không có sự khác biệt có ý nghĩa thống kê ($P = 0.354$, $P = 0.344$) về hình dạng của xương bả vai của 3 loài chà vá. Điều này giúp khẳng định giống *Pygathrix* có đặc trưng riêng về hình dạng của xương bả vai.

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*) are united by a distinct nasal morphology, a high intermembral index (90+), and 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 recognized: the red-shanked douc

langur (*Pygathrix nemaeus*), the grey-shanked douc langur (*P. cinerea*), and the black-shanked douc langur (*P. nigripes*) (Groves, 2001; Roos & Nadler, 2001; Nadler 2014).

Douc langurs are smaller than *Rhinopithecus* and *Nasalis* and are slightly larger than *Simias* (Table 1) (Delson et al., 2000; Smith & 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 suggested by their common names, the 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 territories (Lippold & Vu Ngoc Thanh, 2015; Nadler & Brockman, 2014). *P. nigripes* is found in southern Vietnam and eastern Cambodia, *P. cinerea* in the central highlands of Vietnam, and *P. nemaeus* in east-central Laos, north-central Vietnam and in a very small part of northern Cambodia (Nadler & Brockman, 2014; Rawson et al., 2008; Vu Ngoc Thanh et al., 2008a; Vu Ngoc Thanh et al., 2008b).

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 as all were classified as members of the species *P. nemaeus* (Nadler, 1997). *P. nemaeus* was first described by Linnaeus in 1771. Milne-Edwards (1871) later designated the black-shanked douc as the sub-species *P. nemaeus nigripes*. Finally, in 1997 the grey-shanked douc langur was described as *P. nemaeus cinerea* (Nadler 1997). In 2001, mitochondrial DNA findings motivated the reorganization of *Pygathrix* into the currently recognized set of three species, elevating the subspecies into species (Roos & Nadler, 2001; Roos et al., 2007). The undisputed findings of Roos & Nadler (2001) is one of the bases for the current three species phylogeny. *P. 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 & Nadler (2001) noted phylogenetic structure in the genus, finding *P. nigripes* to be the most basal taxa 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 & Davis, 1959; Napier & 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 & Oxnard, 1963; 1964a; 1964b). In addition to the musculoskeletal studies, it was observed that these colobines would

Table 1. Average male weight for the odd-nosed monkey clade and other African and Asian colobines (Delson et al., 2000; Fleagle, 2013; Smith & Jungers, 1997).

		Weight (kg)
Odd-nosed colobines	<i>Pygathrix</i> spp.	11
	<i>Nasalis larvatus</i>	20
	<i>Rhinopithecus</i> spp.	14 – 20
	<i>Simias concolor</i>	9
African colobines	<i>Colobus angolensis</i>	9.68
	<i>Colobus polykomos</i>	9.9
	<i>Colobus guereza</i>	13.5
	<i>Piliocolobus badius</i>	8.36
Asian colobines	<i>Trachypithecus francoisi</i>	7.7
	<i>Trachypithecus phayrei</i>	7.87
	<i>Trachypithecus johnii</i>	12
	<i>Presbytis melalophos</i>	6.59

leap then use their forelimbs to grasp handholds or check momentum (Napier, 1963). In their classic work, Napier & 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 suggest that the forelimb morphology of *Rhinopithecus* is actually a reflection of climbing rather than arm-swinging (Isler & 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 & Napier (1967).

Category	Sub-type	Genera
Quadrupedalism	Slow climbing type	<i>Arctocebus, Loris, Nycticebus, Perodicticus</i>
	Branch Running and walking type	<i>Aotus, Cacaiao, 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*</i> , <i>Nasalis, Presbytis, Pygathrix, Rhinopithecus, Simias</i>
Brachiation	True brachiation	<i>Hylobates, Symphalangus, Nomascus</i>
	Modified brachiation	<i>Gorilla, Pan, Pongo</i>

* *Colobus* has since been removed from any brachiating locomotor category (Mittermeier & Fleagle, 1976).

Unlike the other odd-nosed colobines, the red-shanked and grey-shanked douc langurs have been regularly observed engaging in brachiation and forelimb suspension in captivity at the Endangered Primate Rescue Center (EPRC), Vietnam (Byron & Covert, 2004; Workman & Covert 2005; Wright et al., 2008]. Byron & 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. nemaeus*, 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 suggested the use of suspensory and brachiation behaviors (Ullbarri, 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 & Oxnard, 1964b; 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 & Oxnard, 1964b; Larson, 1993, Michilsens et al., 2009). Ashton & Oxnard (1964b) 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 & 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 & Covert 2004; Covert et al., 2004).

This study is a preliminary 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). Uniform scapular shape would indicate that the species *P. nigripes* is likely also a semi-brachiator (assuming that scapular morphology is reflective of locomotion in this taxon), an important inference given *P. nigripes*' basal status within the genus. We present preliminary data on the gross scapular shape of the douc langurs.

Material and Methods

Specimens were measured at the Muséum National d'Histoire Naturelle Paris (France) the Dalat Museum (Vietnam), the Southern Institute of Ecology (Ho Chi Minh City, Vietnam), and the Endangered Primate Rescue Center (Vietnam). 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. The first specimen that was broken required imputation for landmarks four and eight. The second broken specimen required imputation for landmark number four

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 (Fig. 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).

Table 3. Species counts.

Species	N	Location
<i>Pygathrix cinerea</i>	14	Kon Ka Kinh Primate Conservation Program (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)

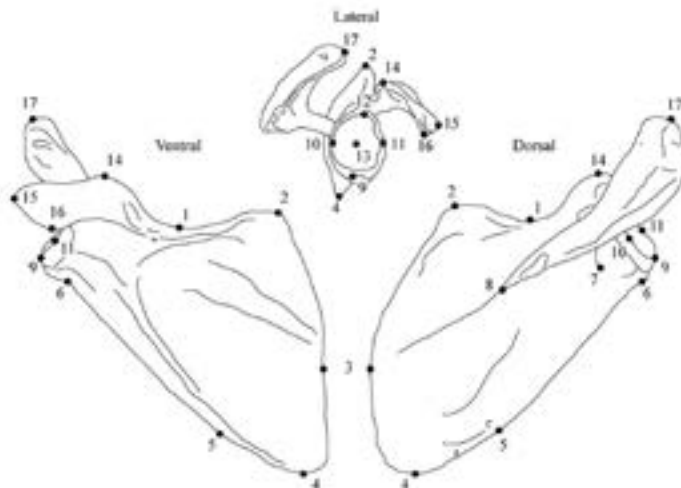


Fig.1. Landmarks used following the methods of Young (2008).

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

No.	Landmarks
1	Suprascapular notch
2	Superior angle
3	Vertebral border and scapular spine intersection
4	Inferior angle
5	Teres major fossa
6	Infraglenoid tubercle
7	Spinoglenoid notch
8	Medial extent of trapezius attachment on scapular spine
9	Inferior extent of glenoid fossa
10	Lateral extent of glenoid fossa
11	Medial extent of glenoid fossa
12	Superior extent of glenoid fossa
13	Central maximum curvature of glenoid fossa
14	Coracoid prominence
15	Superior tip of the coracoid process
16	Inferior tip of the coracoid process
17	Distal-most point of the acromion process.

All data analyses were conducted using the geomorph package in R (Adams & 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.

Results

The Procrustes ANOVA showed no significant difference ($P = 0.354$) between the three species (Table 5). Results of the pairwise group ANOVA also showed no statistically significant differences 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 (Fig. 2). *P. 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. nemaus* 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	p
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

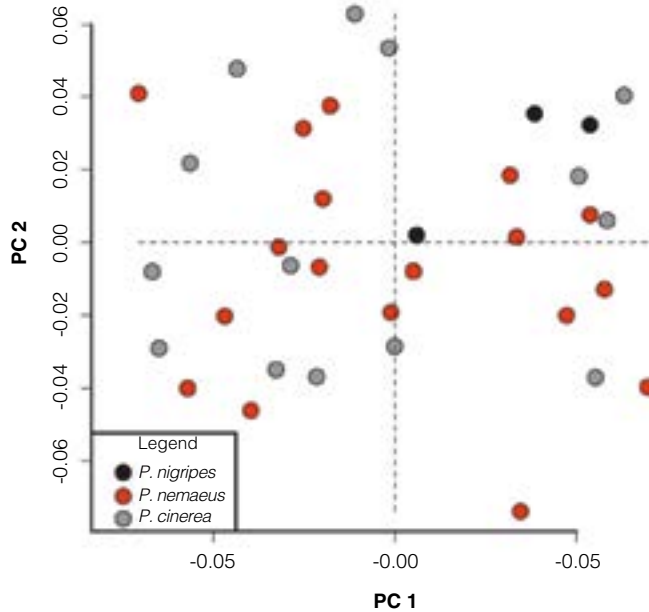


Fig.2. Principle Component Analysis of scapular shape diversity of *Pygathrix* spp.

Discussion

The results presented 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, we speculate that the locomotor behavior of the black-shanked douc is also that of a semibrachiator, despite the lack of direct observation of their locomotion.

The douc langur species have very little 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 m 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 m) (Ulibarri, 2013) whereas the mean height of sleeping trees for the black-shanked douc langur in the Mondulkiri Province, Cambodia was 20.83 ± 3.06 m (Rawson, 2009). The density of vegetation, tree height, and changes in elevation in these differing areas would presumably 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 & Napier, 1967; Young, 2003). Compared to other colobines, the odd-nosed monkeys are typically larger and this could be the eminent factor for the observed divergence and variability in their locomotor patterns as compared to other smaller colobines (Table 1). Arboreal colobines also tend to be significantly larger than their arboreal cercopithecine cousins (Fleagle, 2013), none of which are grouped into Napier & Napier’s (1967) ‘Old World Semi-brachiation’ category (Table 2), whereas Napier & 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 regularly been observed swimming in the mangrove swamps of Indonesia and *Rhinopithecus bieti* is largely terrestrial and is often found slow climbing to maneuver through the trees (Isler & Grüter, 2006; Yeager, 1991). Conversely, *R. avunculus* rarely comes to the ground (Dong Thanh Hai & Boonratana, 2006). 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.

Conclusion

This morphological study shows little to no significant variation between the scapulae of the three *Pygathrix* species. The douc langurs are a particularly understudied group of Old World monkeys (Byron & Covert, 2004). The studies that have been conducted on their locomotor behavior have predominantly been in a captive environment (e.g. Byron & Covert, 2004; Covert et al., 2004; Workman & 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 to identify locomotor patterns in these primates and identify shape variability within the genus. This study also warrants an investigation of the scapular shape of semibrachiators. It is possible semibrachiators, specifically *Pygathrix*, have a unique scapular morphology reflective of their intermediate locomotor category.

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

Michael C. Granatosky

Department of Evolutionary Anthropology, Duke University, Durham, NC, 27708, USA
<michael.granatosky@duke.edu>

Key words: Brachiation, suspensory, locomotion, colobines, experimental biology, pendulum

Summary

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

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

Tóm tắt

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

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

Introduction

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

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

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

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

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

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

Materials and Methods

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

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

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

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

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

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

Results

Kinetic data

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

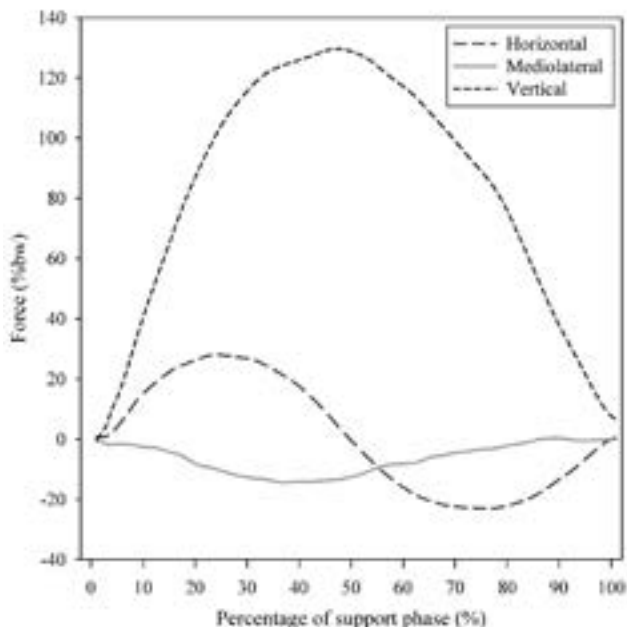


Fig.1. Mean force trace for all strides collected in this study. Positive values in the horizontal force component indicate propulsive forces, while negative values indicate braking forces. Positive values in the mediolateral force component indicate laterally directed forces, while negative values indicate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

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

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

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

Kinematic data

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

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

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

Discussion

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

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

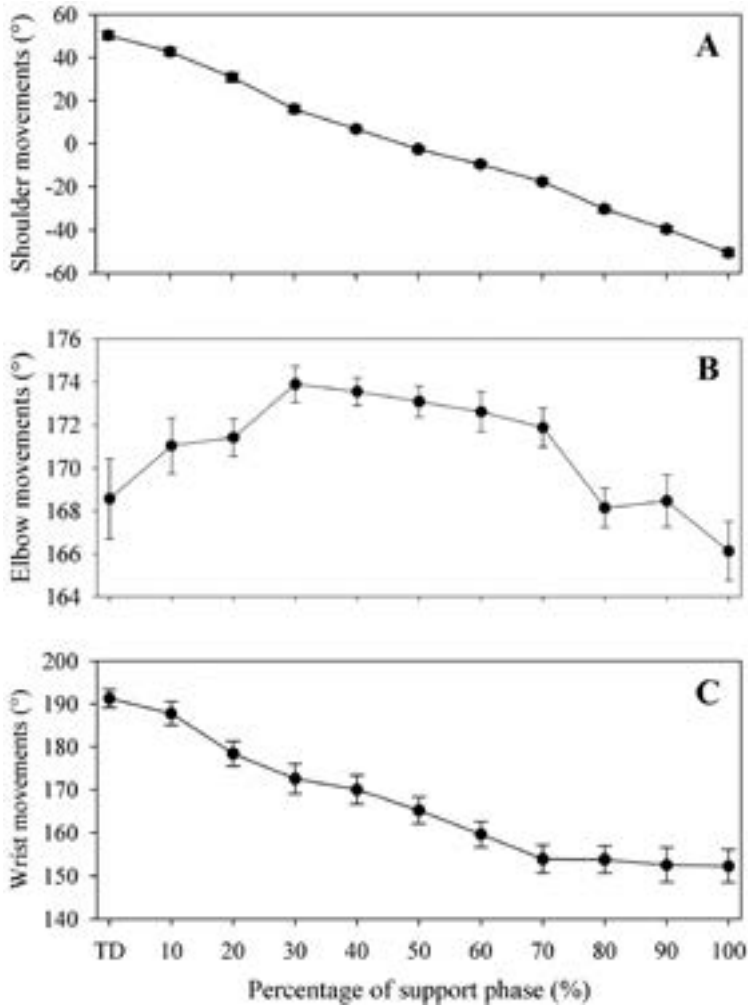


Fig.2. Patterns of shoulder (A), elbow (B), and wrist (C) movements from touchdown (TD) to the end of support phase during arm-swinging in *Pygathrix nemaeus* (mean and standard error). All angular measurements are reported in degrees. Shoulder angles are reported relative to the neutral axis of the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

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

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

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

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

Conclusions

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

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Estimation of northern yellow-cheeked gibbon (*Nomascus annamensis*) population size in Kon Cha Rang Nature Reserve: a new method—using a weighted correction factor

Vu Tien Thinh and Dong Thanh Hai

Forestry University of Vietnam, Xuan Mai, Chuong My, Ha Noi
Corresponding author: Vu TienThinh <vutienthinh@hotmail.com>

Key words: Northern yellow-cheeked gibbon, *Nomascus annamensis*, Kon Cha Rang Nature Reserve, population size, weighted correction factor

Summary

The recently described northern yellow-cheeked gibbon (*Nomascus annamensis*) is endemic to Indochina but the status of the species in Vietnam is still poorly understood. The methods currently used to survey and monitor gibbons do not allow flexible survey designs and often underestimate the numbers of gibbon groups because gibbon groups do not call every day. To determine the status of the species in Kon Cha Rang Nature Reserve in central Vietnam and to contribute to improve methods for field surveys for gibbons and data analysis, we surveyed from 17 listening posts at this site in three weeks from June to July, 2010. During the survey we detected 13 gibbon groups. Daily calling probability was estimated to be 0.3 and the weighted correction factor was estimated to be 0.63. Maximum hearing distance for the gibbon calls was estimated to be about 2 km at this site. The total number of gibbon groups at Kon Cha Rang Nature Reserve was consequently estimated to be 27. These gibbon groups are mainly distributed in the northern part of the reserve.

Ước lượng kích thước quần thể loài Vượn má vàng phía Bắc (*Nomascus annamensis*) tại Khu bảo tồn Kon Cha Răng: Một phương pháp mới sử dụng hệ số hiệu chỉnh có trọng số

Tóm tắt

Vượn má vàng phía Bắc (*Nomascus annamensis*) gần đây được ghi nhận là một loài linh trưởng mới của Việt Nam. Thông tin về tình trạng của loài ở Việt Nam nói chung và Khu bảo tồn thiên nhiên Kon Cha Rang nói riêng còn chưa đầy đủ. Trong điều tra và giám sát vượn, các phương pháp ước lượng hiện đang được sử dụng thường không cho phép việc tổ chức thực hiện điều tra một cách linh hoạt và số đàn vượn ước lượng được thường nhỏ hơn so với thực tế bởi một đàn vượn không phải ngày nào cũng hót. Để xác định tình trạng của loài tại Khu bảo tồn thiên nhiên Kon Cha Rang và góp phần hoàn thiện phương pháp điều tra thực địa và xử lý số liệu trong điều tra giám sát các loài vượn. Chúng tôi tiến hành điều tra tại 17 điểm nghe vượn hót trong thời gian 3 tuần, từ tháng 6 đến tháng 7 năm 2010. Qua đợt điều tra 13 đàn Vượn đã được ghi nhận. Xác suất hót trong một ngày được ước lượng là 0.3 và hệ số hiệu chỉnh có trọng số được ước lượng là 0.63. Khoảng cách lớn nhất mà người điều tra có thể phát hiện ra tiếng hót của vượn được ước lượng vào khoảng 2km và tổng số đàn vượn ở Khu bảo tồn thiên nhiên Kon Cha Rang được ước lượng là 27 đàn. Các đàn Vượn này chủ yếu phân bố ở khu vực phía Bắc của Khu bảo tồn.

Introduction

The northern yellow-cheeked gibbon (*Nomascus annamensis*) is endemic to Indochina and is distributed in southern and central Vietnam, north-eastern Cambodia, and southern Laos. The distribution in Vietnam reaches from the Thach Han River in the North (about 16°40' - 16°50' N) to the Ba River in the South (about 13°00' - 13°10' N) (Van Ngoc Thinh et al., 2010). The species is currently

not listed on the IUCN-Red List of Threatened Species as it has only recently been described (Van Ngoc Thinh et al., 2010). It is likely the species, once listed, will fall within the category 'Endangered' based on the reduction of the population size in recent years due to habitat loss and poaching. However to really clarify the status of the species, efforts must be made to estimate its populations.

Some authors reported that the crested gibbons including northern yellow-cheeked gibbon are fairly common in the Central Highland of Vietnam (Brickle et al., 1998; Geissmann et al., 2000). Located in the Central Highlands region in Gia Lai Province lies Kon Cha Rang Nature Reserve which is believed to support a large population of northern yellow-cheeked gibbons. The presence of gibbons in the nature reserve has been mentioned (BirdLife International & Forest Inventory and Planning Institute, 2001; Geissmann & Orgeldinger, 2000), but adequate efforts have not yet been made to understand the status of gibbons in the reserve. Kon Cha Rang is one of the least disturbed nature reserves in Vietnam, covering an area of 15,472 ha. The forest remains intact or is only slightly disturbed by human activities and creates a very suitable habitat for gibbons. Given its habitat quality and large size Kon Cha Rang Nature Reserve, can support a viable population of northern yellow-cheeked gibbons and serve as an important conservation area for the species. Our survey for this species in the nature reserve will provide a background for conservation of this primate species.

Methods

Study site

Kon Cha Rang Nature Reserve (14°26'-14°35' N/108°30'-108°39' E) is located in K'Bang District, Gia Lai Province. Established in 2000 the total area comprises 15,472 ha. The establishment of a buffer zone of 56,000 ha in Son Lang and Dak Rong Communes in Ang District has been proposed. Kon Cha Rang Nature Reserve borders An Lao Nature Reserve (Binh Dinh Province) to the east and several Forestry Enterprises to the South and West. Soil hills characterize the topography of the reserve, and the elevation ranges between 800 m and 1,152 m asl, with the highest peak Kon Cha Rang at 1,159 m (BirdLife International & Forest Inventory and Planning Institute, 2001). In the northern part of the reserve many peaks reach elevations of more than 1000 m asl.

62 mammal species, 169 bird species and 161 butterfly species have been recorded in the reserve. Notably, the presence of several globally endangered mammals such as *Nomascus annamensis*, *Pygathrix cinerea*, and *Megamuntiacus vuquangensis* have been recorded within the reserve (Anon., 1999; BirdLife International & Forest Inventory and Planning Institute, 2001; Nadler et al., 2003)

Of its 15,472 ha, 13,844.2ha (89.5%) are rich and medium forest and 1627.8 ha (10.5%) are degraded forest or bare land. Of 15,472 ha of rich and medium forest, 70-80 % is tropical evergreen broadleaf forest. The main plant families are Fagaceae, Lauraceae, Magnoliaceae. Mixed forest with broad-leaved and coniferous species such as *Podocarpus imbricatus* and *Dacrydium elatum* also occurs.

Selection of survey areas

According to interview information, gibbons used to be abundant in the northern and central parts of the reserve. These areas, especially the northern part, are also least disturbed by previous logging. The southern part of the reserve has been logged since 1970 by Tram Lap Forestry Enterprise and doesn't provide a good habitat for gibbons. Local people reported that gibbons have not been seen in this area recently. Therefore, we decided to focus our surveys on the northern and central parts of the reserve (Fig. 1).

Survey method

Gibbons live in the upper forest canopy and are mostly sensitive to human presence. Therefore, visual detection of gibbons is very difficult in the field, especially in short surveys. However, gibbons can be detected by their loud and long songs (Geissmann, 1993; Geissmann & Orgeldinger, 2000). Therefore, an audio point counting method was used to assess gibbon population size and density during the survey (Brockelman & Ali, 1987).

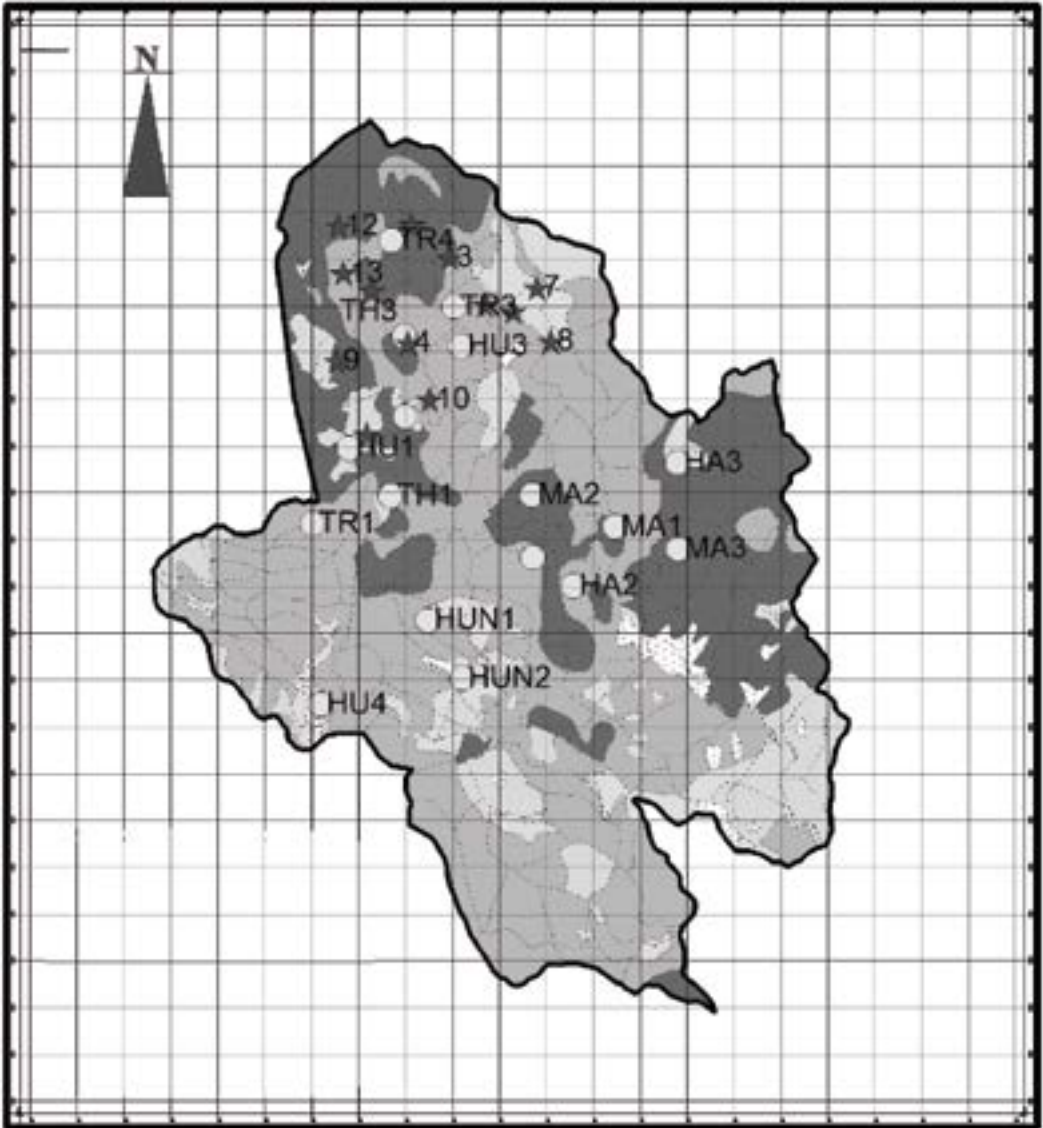


Fig.1. Map of Kon Cha Rang Nature Reserve with listening posts (o) and detected gibbon groups (★).

A total of six camp sites were used during the survey, all of which were located inside the nature reserve. A total of 17 listening posts were selected (Fig. 1), covering an area of 10,250 ha (radius per post 2 km), of which 9,372 ha were included in the nature reserve. Transects were not conducted in this survey due to difficult terrain and inefficiency of this method for gibbon surveys. This method also tends to underestimate gibbon density (Brockelman & Ali, 1987).

Of 17 posts used, 13 posts were surveyed for two days, two posts were surveyed for three days, and two posts were surveyed for one day. Surveys were conducted in the morning (5:00 to 9:00am), from 17th June to 15th July 2010. During the surveys, the surveyors took a compass bearing of the direction of the group, estimated the distance to the group, and recorded the start and end time of all song bouts, and the type of song.

Data analysis

Locations of gibbon groups could be determined by triangulation using the angle and distance from different surveyors as the areas covered from different listening posts overlapped (Fig. 2). The distance was measured using MapInfo 10.0 (Pitney Bowes Business Insight, New York, US). Maximum hearing distance was estimated using the recorded distance between surveyors and gibbon locations with known coordinates. When gibbon groups were heard by at least two surveyors in the same day, the distance between the surveyors and these gibbon groups could be estimated rather accurately. If the third surveyor could not hear the songs of the identified groups on that day, the minimum distance at which song cannot be detected was also identified. Based on these two distances measured for several groups, the maximum hearing distance for this site was determined. Maximum hearing distance was then used to calculate the area surveyed.

Groups were differentiated by their locations; they were considered separate groups if they were detected more than 500 m apart, and group density was then estimated (Brockelman & Ali, 1987).

Using a “common” correction factor as widely accepted might be problematic. In gibbon surveys it is difficult to avoid overlapping survey area across posts. If two adjacent posts are surveyed in different days, then the overlapping areas are surveyed in more days than non-overlapping areas. Therefore, estimation using a common correction factor might be positively biased. The estimate of gibbon group might be higher than the truth. This issue is of critical importance if the overlapping area is large compared to non-overlapping areas. Therefore, we propose using a “weighted correction factor”. Additionally, the weighted correction factor also allowed for flexibility in survey design. Different effort might be applied to different listening posts (Fig. 3).

The “weighted correction factor” is calculated as follows:

$$WC = \frac{\sum_{i=1}^m a_i \cdot C_i}{A}$$

WC: weighted correction factor

C: correction factor

a_i : area surveyed in i days

C_i : correction factor applied for area surveyed i days,

A: total area surveyed

m : maximum number of days surveying an area during the study

C_i is calculated as: $C_i = 1 - (1 - p_1)^i$

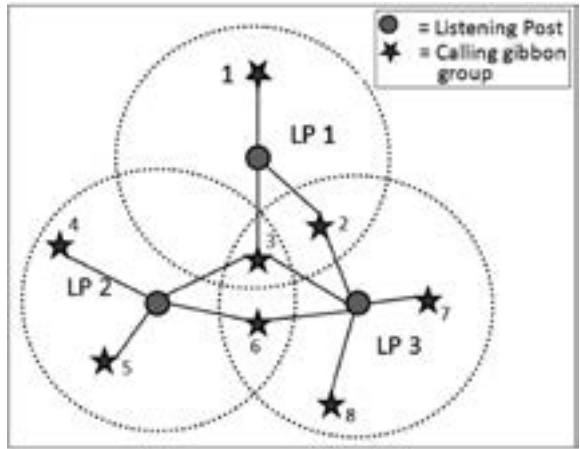


Fig.2. Survey design for the arrangement of listening posts.

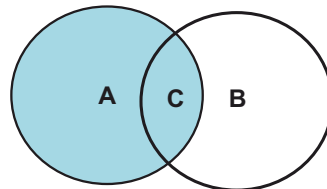


Fig.3. Explanation to the weight correction factor.

Area A is surveyed for only one day: Correction factor: $1 - (1 - 0.3) = 0.3$

Area B is surveyed for 2 days: Correction factor: $1 - (1 - 0.3)^2 = 0.49$

Area C is surveyed for 3 days: Correction factor: $1 - (1 - 0.3)^3 = 0.657$

The correction factor is always <1.

The number of gibbon groups in the surveyed areas was estimated by dividing the number of detected groups by the weighted correction factor. The number of groups in Kon Cha Rang Nature Reserve was then extrapolated based on density and habitat size.

Results

Number of northern yellow-cheeked gibbons

Based on interview information, gibbons were in the past abundant in the northern and possibly the central parts of the reserve. Local people also reported that no gibbons have been recently recorded in the southern part of the reserve. The southern part of the reserve was heavily disturbed by previous logging activities and might no longer be a suitable habitat for gibbon.

During the survey gibbon songs were heard from 20 locations near Kon River, Nuoc Reo, Suoi Reu and Suoi Bom Streams. Most of the locations from which songs were detected were located in the very northern part of the reserve, covering an area of about 4,000 ha. Of that, 3100 ha lies in the sampled area around the listening posts. These areas include 31, 32, 33, 34, 35, and 36 forest compartments.

From the 20 locations at least 13 different groups of gibbons were identified (Fig. 1). Some groups, recorded from different locations on different days were probably the same groups because the distances between the listening locations were relatively short.

Maximum hearing distance

Five gibbon groups were heard from at least two posts on the same day. Therefore, their exact locations could be determined by triangulation. Recorded hearing distances ranged from 300 m to 1800 m (Table 1). In three cases, the surveyors recorded the songs of gibbons at a distance of around 1800 m with a volume level ranging from two to three. We concluded that the maximum hearing distance in this survey may be more than 1800 m. In three other cases, surveyors failed to detect the gibbon songs at distances of more than 2100 - 2200 m. Consequently the maximum hearing distance in this survey lay between 1800 and 2100 m. We arbitrarily selected 2000 m as the maximum hearing distance for our calculations.

Table 1. Distance from observers to gibbon locations with known coordinates.

Gibbon group ID	Post ID	Date	Distance (m)	Volume level	Estimated distance in the field (m)	Note
1	HU1	18/6	300m	1	<500	Heard
	TH1		1400	2	800	Heard
	TR1		2100			Not heard
2	HU3	21/6	1300	2	<2000	Heard
	TR3		1400	2	1000	Heard
	TH3		2400			Not heard
3	HU3	21/6	1800	2	<2000	Heard
	TH3		1800	2.5	2000	Heard
	TR3		900	2	1000	Heard
4	HU3	23/6	1200	1	1500	Heard
	TR3		1300	2	500-1000	Heard
	TR4		2200			Not heard
5	TR3	23/6	1800	3	1500	Heard
	TR4		1200	1	1500	Heard
						Not heard

Volume level: 1 = Loud; 2 = Medium; 3= Slight

Estimated population size of northern yellow-cheeked gibbons

Based on data from 11 groups that were detected on at least 3 days we estimated the probability of singing in one day (p_1) following Jiang et al. (2006).

This data amounted for our area to an estimation of singing probability in one day of $p_1 = 0.30$. This estimate was then used to calculate the correction factor.

As the probability of a gibbon group singing on a single day is smaller than one, the actual number of gibbon groups is higher than the number of groups heard during the survey. The actual number of groups within surveyed areas was estimated by dividing the number of groups heard by a correction factor.

Survey efforts vary among areas of the reserves (Table 2). A total of 9,372 ha of habitat in the reserve was surveyed. The area surveyed in more than one day was 8,728 ha. The weighted correction factor is 0.63 (Table 2). Therefore, the estimated actual number of groups within the surveyed area is $13/0.63 = 20.66$ (≈ 21 groups).

Of the 4,000 ha of probable gibbon distribution range in the reserve, the survey covered about 3,100 ha, and about 900 ha were not surveyed. Therefore, the total number of gibbon groups in the reserve is estimated to be 26.66, about 27 groups. The density of northern yellow-cheeked gibbons in its distribution range of 4,000 ha in Kon Cha Rang Nature Reserve is 0.0066 groups/ha (0.66 groups/km²). The density of northern yellow-cheeked gibbons in the entire surveyed area of 9,372 ha is 0.0022 groups/ha (0.22 groups/km²).

Discussion

Distribution of northern yellow-cheeked gibbons in Kon Cha Rang

Information about the distribution of northern yellow-cheeked gibbons collected from interview and field survey was similar. This meant that local informants had been selected well and obtained interview information that was useful for further design of the survey.

Within Kon Cha Rang northern yellow-cheeked gibbons are now confined to a small area of about 4,000 ha in the North of the reserve. This is probably because this area is remote and there is less poaching than in other parts of the reserve and the forest quality in this area is better than in the central and southern parts of the reserve, which have been selectively logged in the past.

Density and population size

The density of gibbons in Kon Cha Rang Nature Reserve was found to be much higher than in the North Central coastal region of Vietnam (Nguyen Manh Ha et al., 2005). In Dak Rong Nature Reserve the density of gibbons was estimated to be only 0.06 groups/km², though this area is considered to have the highest gibbon density in the North Central coastal region of Vietnam (Nguyen Manh Ha et al., 2005). This implies that efforts to conserve northern yellow-cheeked gibbons in Vietnam should focus on southern parts of the species' distribution range, including the Central Highland as this region is still supporting viable populations.

The population of northern yellow-cheeked gibbons in Kon Cha Rang Nature Reserve and other protected areas in Vietnam is much smaller than in other countries within the distribution range of this species. In Cambodia, the population in Virachey National Park (332,500 ha), Cambodia, was estimated to comprise about 5,750 groups and the population in Pheapimex Concession (315,028 ha) about 1,100 groups (Traeholt et al., 2005).

Although Kon Cha Rang Nature Reserve is smaller than these protected areas, it is obvious that the population densities in these areas are much higher. Low hunting pressure and less habitat disturbances due to smaller human population density may be the major reason for the greater population sizes of northern yellow-cheeked gibbons found in Lao PDR and Cambodia.

Determination of maximum hearing distance

To estimate the maximum hearing distance is essential in order to extrapolate the number of gibbon groups in the whole nature reserve based on the estimated number of gibbon groups in

surveyed areas. The maximum hearing distance was used to calculate the “weighted correction” factor, which has not been used in previous publications.

The maximum hearing distance allows for calculating overlapping survey areas.

To estimate a common maximum hearing distance, the following conditions must be met:

- All teams have the same hearing capacity.
- Sound transmission is uniform among different areas of the reserve.
- Weather does not influence hearing ability.

In our survey, all conditions were met. All teams have two surveyors, of that at least one will have experience in detecting gibbon songs.

In Table 1, the minimum distance from which the surveyors cannot detect the gibbon groups is rather similar. In a study where the survey teams have different degrees of experience, the maximum hearing might differ between survey teams and must be estimated separately for each group. However, this would require much more survey efforts. Other solutions would be to keep the number of survey teams small and survey over a longer survey period or stratify surveyors by their experience.

The terrain in Kon Cha Rang Nature Reserve is uniform; therefore, we believe that the maximum hearing distance does not vary much among the areas surveyed. The survey was conducted in a short period and the weather in the mornings of all survey days was similar. In other surveys conducted in longer period, days with bad weather should be excluded from maximum hearing distance analysis.

Estimation of the correction factor

The estimation of calling probability in one day was 0.30. Therefore, correction factor for a two day survey and a three day survey was 0.50 and 0.65, respectively. This estimate was small compared to other studies (Jiang et al., 2006; Phanchana & Gray, 2009). These authors reported the correction factor of around 0.90 for a three day survey. The lower correction factor in this study is probably due to the small sample size and the small estimate might result from chance alone. Furthermore the density of gibbons in Kon Cha Rang Nature Reserve is lower than in other studies, therefore, the singing probability may be low due to lack of stimulation from other groups (Raemaekers & Raemaekers, 1985). In addition, using 500 m distance as the threshold to differentiate two groups (Brockelman & Ali, 1987) may be incorrect as northern yellow-cheeked gibbons might have large home ranges in Kon Cha Rang Nature Reserve. Larger home ranges may be possible because of low density and conspecific competition. If one group is considered two separate groups, estimates of singing probability will be lower. Rawson (2004) suggested vocalizations of southern yellow-cheeked gibbons in Cambodia would be less frequent in the raining season (May to October in the Central Highland of Vietnam). This survey was conducted in June and July, therefore the singing probability might be lower than average. Finally, higher hunting pressure in Kon Cha Rang Nature Reserve compared to other areas may lead gibbons to call less frequently than usual.

Using a common correction factor as widely accepted might be problematic, even when survey efforts do not vary between posts. In gibbon surveys, it is difficult to avoid the overlap of areas covered from various listening posts. If two adjacent posts were surveyed in different days, then the overlapping areas are surveyed for more days than non-overlapping areas. Therefore, estimation using a common correction factor might be positively biased resulting in estimates of gibbon group numbers which might be higher than the truth. This is of critical importance if the overlapping area is large compared to areas covered only from one listening post. In this study we used singing probability of 0.30 (in one day). Theoretically, the detection probability in a period of two days is 0.50, in three days is 0.65, and in four days is 0.75 (Table 2). In our study most of the area (82%) was investigated for two to four days. Specifically, 35%, 19%, and 28% of the area was investigated for two days, three days, and four days, respectively. With the weighted correction factor of 0.63, we believed that the correction factor is reasonable. More importantly, the “weighted correction factor” allows for flexibility in survey design.

Table 2. Survey effort allocation and calculation of weighted correction factor.

Number of days	1	2	3	4	5	6	7	8	Total
Area (ha)	644.2	3313.9	1746.9	2581.4	105.4	899.4	0	80.7	9372
Correction factor	0.30	0.50	0.65	0.75	0.83	0.88	0.91	0.94	0.00
Weighted correction factor calculation	0.02	0.18	0.12	0.21	0.01	0.08	0.00	0.01	0.63

Conclusions

During the survey 13 gibbon groups were detected. Gibbons are now confined to a small area in the northern part of Kon Cha Rang Nature Reserve. Daily calling probability was estimated to be 0.3 and a “weighted correction factor” was estimated to be 0.63.

The total number of gibbons groups within Kon Cha Rang Nature Reserve is estimated to be 27.

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INSTRUCTIONS FOR CONTRIBUTORS

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Submission: Submit English manuscripts electronically (as unformatted Microsoft Word file attachments) to Tilo Nadler or Christian Roos:

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Endangered Primate Rescue Center	German Primate Center
Vietnam	Germany
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The first page of the manuscript should include the complete title of the paper, the authors' names, an abstract and key words. The complete postal addresses, e-mails and affiliated institutions of the authors must be given at the bottom of the title page.

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Research articles and short communications must be organized into the following sections: Introduction, Materials and Methods, Results, Discussion, Conclusions, Acknowledgements and References. Acknowledgements may include funding sources such as agency and grant numbers, and the names of those who contributed.

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Fooden J (1996): Zoogeography of Vietnamese Primates. *Int. J. Primatol.* 17, 845-899.

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Groves CP (2001): *Primate Taxonomy*. Washington DC.

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Groves CP 2004: Taxonomy and Biogeography of Primates in Vietnam and Neighbouring Regions. In: Nadler T, Streicher U. & Ha Thang Long (eds.): *Conservation of Primates in Vietnam*; pp. 15-22. Frankfurt Zoological Society, Hanoi.

Dissertations

Otto C (2005): Food intake, nutrient intake, and food selection in captive and semi-free Douc langurs. PhD thesis, University Cologne, Germany.

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