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Impending extinction crisis of the world's primates: Why primates matter

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Key words: nonhuman primates, tropical forests, deforestation, hunting, illegal trade, primate conservation, sustainable land use, industrial agriculture, ecosystem health, rural livelihoods

Abstract

Nonhuman primates, our closest biological relatives, play important roles in the livelihoods, cultures, and religions of many societies and offer unique insights into human evolution, biology, behavior, and the threat of emerging diseases. They are an essential component of tropical biodiversity, contributing to forest regeneration and ecosystem health. Current information shows the existence of 504 species in 79 genera distributed in the Neotropics, mainland Africa, Madagascar, and Asia. Alarmingly, ~60% of primate species are now threatened with extinction and ~75% have declining populations. This situation is the result of escalating anthropogenic pressures on primates and their habitats - mainly global and local market demands, leading to extensive habitat loss through the expansion of industrial agriculture, large-scale cattle ranching, logging, oil and gas drilling, mining, dam building, and the construction of new road networks in primate range regions. Other important drivers are increased bushmeat hunting and the illegal trade of primates as pets and primate body parts, along with emerging threats, such as climate change and anthroponotic diseases. Often, these pressures act in synergy, exacerbating primate population declines. Given that primate range regions overlap extensively with a large, and rapidly growing, human population characterized by high levels of poverty, global attention is needed immediately to reverse the looming risk of primate extinctions and to attend to local human needs in sustainable ways. Raising global scientific and public awareness of the plight of the world's primates and the costs of their loss to ecosystem health and human society is imperative.

Sắp xảy ra cuộc khủng hoảng tuyệt chủng của các loài linh trưởng trên thế giới: Tại sao các loài linh trưởng quan trọng

Tóm tắt

Nonhuman primates (primates hereafter) are of central importance to tropical biodiversity and to many ecosystem functions, processes, and services. They are our closest living biological relatives, offering critical insights into human evolution, biology, and behavior and playing important roles in the livelihoods, cultures, and religions of many societies. Unsustainable human activities are now the major force driving primate species to extinction. Here, we combine the most frequently used standard for species conservation status [the International Union for Conservation of Nature (IUCN) Red List] with data from peer-reviewed scientific literature and from the United Nations databases to evaluate human-induced threats to primate survival. We examine trends in forest loss resulting from regional and global economic pressures and discuss the impacts of hunting, illegal trade, and other anthropogenic threats on primate populations. We also model agricultural expansion into the 21st century and identify expected spatial conflict within primate range areas. We assess the current level of scientific knowledge available for individual primate taxa, and we highlight the ecological, social, cultural, economic, and scientific importance of primates, as well as the global consequences of their population declines. We also consider future research needs and advances in technology for monitoring human-induced environmental changes that affect primate populations. Finally, we propose a conceptual model to guide the development of global, regional, and local approaches to promote primate conservation while at the same time attending to human needs. The goal of this review is not to produce a list of threats but rather to urge attention to the multiple global and regional anthropogenic factors that imperil primates worldwide and to encourage the development of sustainable and effective solutions that enhance primate survival in the medium and long term.

IMPENDING DEFAUNATION OF THE WORLD'S PRIMATES

The order Primates is one of the most species-rich groups of mammals, surpassed only by the orders Chiroptera (bats, 1151 species) and Rodentia (rodents, 2256 species) (1, 2). The most recent taxonomic compilation (April 2016) lists 701 extant taxa belonging to 504 species from 79 genera and 16 families (tables S1 to S4 and Supplementary Text) (2–5). Primates occur in four regions - the Neotropics (171 species), mainland Africa (111 species), Madagascar (103 species), and Asia (119 species) (Fig. 1) - and are present naturally in 90 countries; however, two-thirds of all species occur in just four countries - Brazil, Madagascar, Indonesia, and the Democratic Republic of the Congo (DRC) (figs. S1 and S2A). These countries represent high-priority areas for primate conservation. The large majority of primates inhabit tropical moist lowland forests, but they also occur in tropical dry forests, mangrove vegetation above high-tide levels, moist montane forests, high-elevation (from 1000 to >4000 m) deciduous and broadleaf temperate forests, savannas, grasslands, inland wetlands, rocky areas, and even deserts (2, 4). The body mass of living primates ranges from 30 g in Madame Berthe's mouse lemur (*Microcebus berthae*) to about 200 kg in male western and eastern gorillas (*Gorilla gorilla* and *Gorilla beringei*, respectively) (Supplementary Text) (2, 4, 5).

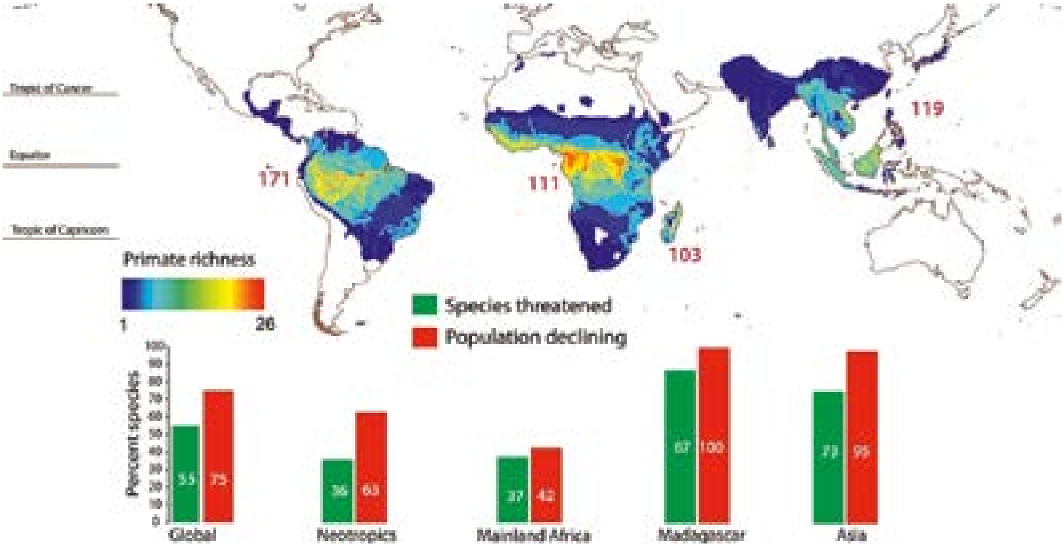

Fig.1. Global primate species richness, distributions, and the percentage of species threatened and with declining populations. Geographic distribution of primate species. Numbers in red by each region refer to the number of extant species present. The bars at the bottom show the percent of species threatened with extinction and the percent of species with declining populations in each region. Percentage of threatened species and percentage of species with declining populations in each region from tables S1 to S4. Geographical range data of living, native species from the IUCN Red List (www.iucnredlist.org) are overlaid onto a 0.5o resolution equal-area grid. In cases in which a species' range was split into multiple subspecies, these were merged to create a range map for the species. Mainland Africa includes small associated islands.

Using information from the IUCN and our current assessment, we estimate that ~60% of primate species, from all 16 extant families, are threatened with extinction because of unsustainable human activities (Figs. 1 and 2 and tables S1 to S4). Threats to primates are widespread: 87% of species in Madagascar are threatened, as are 73% in Asia, 37% in mainland Africa, and 36% in the Neotropics (Fig. 1 and figs. S2B and S3A). The populations of 75% of primate species are decreasing globally (Fig. 1 and fig. S3B). Considering the large number of species currently threatened and experiencing population declines, the world will soon be facing a major extinction event if effective action is not implemented immediately.

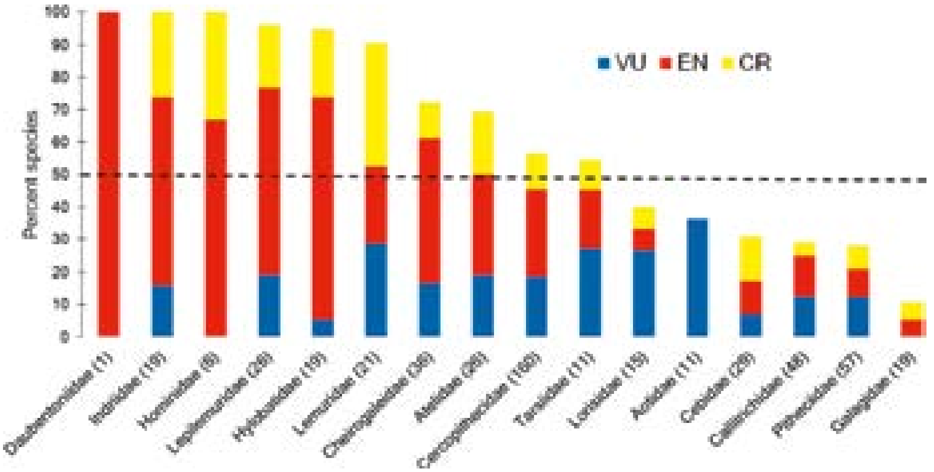

Fig.2. Percent of species threatened with extinction in each primate family.

Assessment of threat level is according to the IUCN Categories and Criteria VU (Vulnerable), EN (Endangered), and CR (Critically Endangered). Number in parentheses after each family indicates the number of species recognized in the family. Data for each species are indicated in tables S1 to S4. Notably, there are threatened species in all 16 primate families. Ten families have more than 50% of their species threatened (broken line at 50%). Note that the graph is only for the Threatened IUCN categories. Families not showing 100% values may have some species classified as Near Threatened (NT), Least Concern (LC), Data Deficient (DD), and Not Evaluated (NE) (see tables S1 to S3). Upon revision of the taxonomy of Malagasy lemurs, a number of taxa once thought to be widespread are now highly threatened; a similar scenario is envisioned for the galagids, where there appears to be a large number of newly recognized species with limited ranges. Taxonomy is based on previous works (*1–3*).

FACTORS THAT THREATEN PRIMATE POPULATIONS

The IUCN indicates that the main threats to primate species are loss of habitat due to agriculture (76% of species), logging and wood harvesting (60%), and livestock farming and ranching (31%), as well as direct loss due to hunting and trapping (60%) (fig. S4A). Other threats, such as habitat loss due to road and rail construction, oil and gas drilling, and mining, affect 2 to 13% of primate species, and there are also emerging threats, such as pollution and climate change (fig. S4B and table S5). Globally, agriculture is the principal threat, but secondary threats vary by region. For example, livestock farming and ranching negatively affect 59% of primate species in the Neotropics. In contrast, in mainland Africa, Madagascar, and Asia, hunting and trapping affect 54 to 90% of the species. Logging is the third greatest threat to primates in all regions (fig. S4A).

Land-cover changes, global market demands, and industry-driven deforestation

Global market demands for nonarboreal (for example, soybeans, sugar cane, and rice) and arboreal crops (for example, oil palm and natural rubber), livestock (particularly cattle), and tropical hardwoods have resulted in a process of rapid and widespread industry-driven deforestation in the Neotropics, mainland Africa, Madagascar, and Asia (Supplementary Text and fig. S5, A to F) (*6*). For example, between 1990 and 2010, agricultural expansion in primate range regions was estimated at 1.5 million km^2 (an area three times that of France) and forest cover loss at 2 million km^2 (Fig. 3 and fig. S6, A to C). Increasing global demand for oil palm products is a major driver of recent severe declines in Sumatran and Bornean orangutan

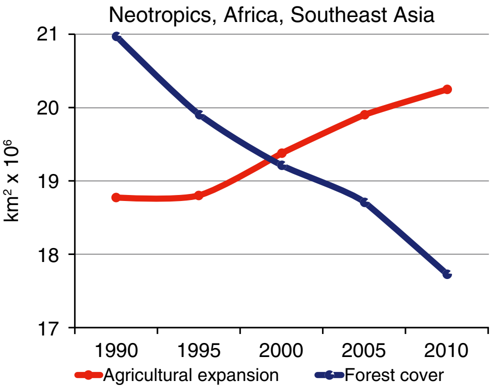

Fig.3. Agricultural expansion and declines in forest cover for the period 1990–2010 in primate range regions.

A rapid expansion of agriculture in primate range regions has been paralleled by a sharp decline in forest cover in the 20-year period considered. Trends for each individual region are shown in fig. S6 (A to C). Data for Africa include Madagascar (source of raw data, FAOSTAT: faostat.fao.org/site/377/DesktopDefault.aspx?PageID=377#ancor. Consulted June 2016).

(*Pongo abelii* and *Pongo pygmaeus,* respectively) numbers and a serious risk for African apes because large segments of existing populations occur outside protected areas (*7–10*). Moreover, future oil palm development is likely to threaten forested areas in South America and Africa (*10*), which is projected to result in severe negative consequences for primate populations in those regions (fig. S5C). The expansion of rubber plantations in southwest China has caused the near extinction of the northern white-cheeked crested gibbon (*Nomascus leucogenys*) and the Hainan gibbon (*Nomascus hainanus*) (*11*). Similarly, deforestation due to the establishment of rubber plantations in India is reported to have severely affected the Bengal slow loris (*Nycticebus bengalensis*), the western hoolock gibbon (*Hoolock hoolock*), and Phayre's langur (*Trachypithecus phayrei*) (*11, 12*). Modeling the overlap between primate species' distributions and forecasted future agricultural production for the 21st century indicates that regions predicted to undergo the greatest agricultural expansion over the next decades comprise 68% of the global area currently occupied by primates (Fig. 4). This will result in unprecedented spatial conflict with 75% of primate species worldwide (Supplementary Text). Therefore, the implementation of policies to divert agricultural expansion to areas where it is likely to result in the least environmental impacts is essential to reduce spatial conflicts between primate-rich areas and the expanding agricultural frontier (*13*).

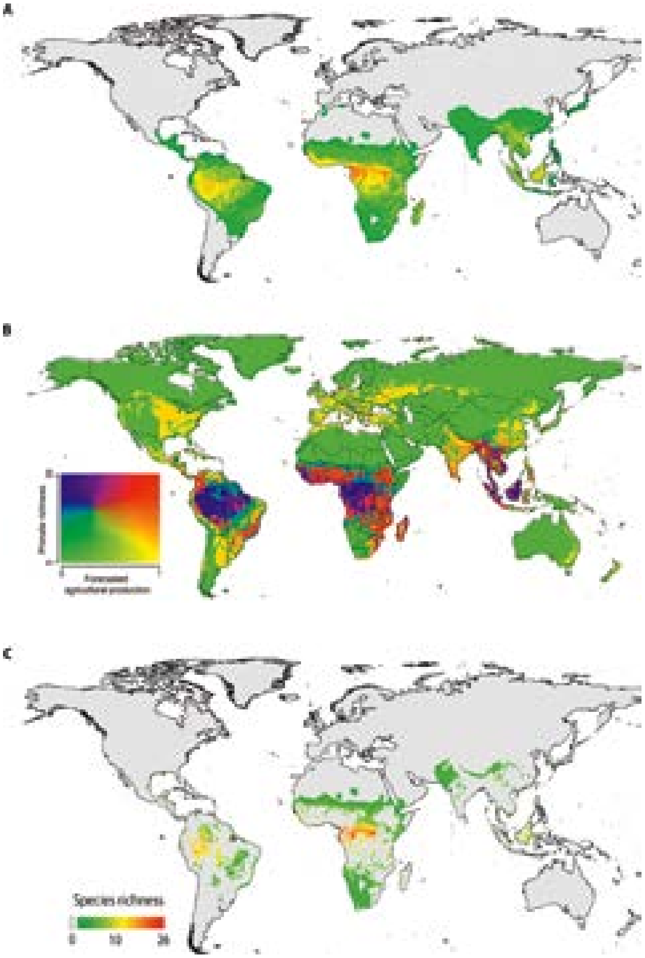

Fig.4. Global patterns of forecasted agricultural expansion for the 21st century in primate range regions and estimated range contraction. (**A**) Estimated current global primate distributions. (**B**) The predicted 21st century expansion of agriculture estimates a spatial overlap with about 75% of primate species habitat worldwide. Red areas indicate higher spatial overlap between agricultural expansion and primate habitat. Blue areas indicate limited spatial conflict. Agricultural expansion represents a synthesis of the expected increase in the location and area devoted to agricultural production, according to the land-cover map produced by the Integrated Model to Assess the Global Environment and potential productivity obtained from the Global Agro-Ecological Zones (Supplementary Text) (*13*). (**C**) Estimated range contraction in primate distributions by the end of the 21st century under a worst-case scenario of agricultural expansion. See Supplementary Text for methods.

Logging, mining, and fossil fuel extraction

Globalized financial markets and a worldwide commodity boom have led to an ever-growing demand for tropical timber and a concomitant expansion of industrial logging, resulting in deforestation and creating a potent economic impetus for road building in forested areas (Supplementary Text) (*14*). Countries in primate range regions are responding to global market demands by expanding logging activities to increase economic growth. In 2010, the Neotropics accounted for 48% of the production of industrial hardwood, followed by Southeast Asia (23%), sub-Saharan Africa (16%), and South Asia (13%) (fig. S5E). In Madagascar, the large-scale harvesting of rosewood (*Dalbergia*) since 2009 has negatively affected several protected areas (*15*). The immediate and long-term effects of legal and illegal logging are a reduction of canopy cover, the destruction of forest undergrowth, and the decline of large tree species important to primates as sources of food and shelter (*16*).

Mining for minerals and diamonds is also a growing threat to tropical ecosystems and their primates. Although it involves relatively small areas, mining contributes to deforestation, forest degradation, and the pollution and poisoning of streams and soil (*17*). In central Africa, the population densities of apes in mined forests [75.7 (45.35 to 126.33) nests/km^2] are markedly lower than in forested sites where mining is absent [234 (185 to 299) nests/km^2] (*18*). In Madagascar, illicit gold and sapphire mining by itinerant miners has affected many forests, including protected ones (*19*). Mining of gold, nickel, and copper on Dinagat island, in the Philippines, is endangering the survival of the Philippine tarsier (*Carlito syrichta*) (*20*). Bushmeat hunting associated with the mining of coltan, tin, gold, and diamonds in the DRC is the main threat to Grauer's gorilla (*G. beringei graueri*) (*21*); recent surveys indicate a 77% decline in its numbers, from 17,000 in 1995 to just 3800 in 2014/2015 (*22*). In Perú, the mining of zinc and copper threatens the endemic and Critically Endangered yellow-tailed woolly monkey (*Lagothrix flavicauda*) (*23*). Development associated with fossil fuel extractions also jeopardizes primate survival. By 2035, global demand for oil and natural gas is projected to increase by >30 and 53% respectively, and primate-rich areas, such as the western Amazon and the western Pacific Ocean (Malaysia, Borneo) will be adversely affected. It is estimated that oil and gas concessions in the western Amazon, and in remote forested areas of Colombia, Ecuador, Brazil, Perú, and Bolivia, already cover about 733,414 km^2 (twice the size of Germany) (*24*).

Other anthropogenic stressors

The expansion of industrialized agriculture, logging, mining, oil/gas extraction, and the building of dams and power-line corridors in tropical forest areas is expected to increase human transportation road networks by some 25 million km by 2050 (Supplementary Text) (*25*). Consequences of the unrestricted road and rail building include increased forest losses from human population migration, illegal colonization, and logging; increased bushmeat hunting; and the illegal wildlife trade (Supplementary Text) (*26*). The construction of conventional dams and megadams for generating electricity to attract energy-intensive industry and stimulate local productivity in the world's most biodiverse river basins—the Amazon, Congo, and Mekong—also poses a severe threat to local primate persistence (*27*). For example, the development of 12 megadams in the state of Sarawak, Malaysia, is expected to result in the loss of at least 2425 km^2 of forest cover, affecting populations of the Endangered Müller's gibbon (*Hylobates muelleri*) (*28*).

Currently, primates feeding on crops (commonly termed "crop raiding") is not considered a major cause of global primate population declines by the IUCN because much of the conflict is local in its occurrence, impact, and the types of crops and primate species affected (*9, 29–33*). There are areas of the world, such as parts of North Africa and Asia, where humans tolerate primates as crop pests because of religious beliefs, cultural traditions, and economic benefit (29). For example, in the Lindu highlands and Buton island of Sulawesi, humans are tolerant of crop feeding macaques due to the role the macaques hold in the local folklore and because they can help in the harvesting of certain crops, such as cashews, where the monkeys eat only the fruit and let the nut fall to the ground to be collected by farmers (*29*). In other cases, crop feeding by primates (for example, howler monkeys) is tolerated without any economic reward (*30*). Where human and nonhuman primates come into more severe conflict due to crop raiding [for example, chimpanzees (*Pan troglodytes*), gorillas (*Gorilla* spp.), and baboons (*Papio* spp.) in Africa and orangutans (*Pongo* spp.) in Southeast Asia] (*9, 31–33*), culturally and economically appropriate management interventions can mitigate the impact (*9, 33*). Human-primate conflict due to primates feeding on crops remains a persistent problem and is likely to increase because primate-suitable habitat is converted into agricultural fields or gardens in response to local and global market demands (Fig. 4).

Civil unrest also affects primate populations because of saturation bombing, the use of defoliating chemicals (*34, 35*), and the increase in bushmeat hunting. Poaching of bonobos (*Pan paniscus*) and gorillas, for example, markedly increased in the DRC and Rwanda as a result of ongoing civil wars (*34*). In Cambodia, armed conflicts have severely affected populations of the black-shanked douc (*Pygathrix nigripes*) (*35*). Land mines, the legacy of wars in the 1960s and 1970s, continue to endanger apes in Southeast Asia and Africa (*34, 36*).

Forest fragmentation and degradation and the limited resilience of primates

Long-term deforestation has resulted in the fragmentation of 58% of subtropical and 46% of tropical forests (*37, 38*), forcing primates to live in isolated forest patches, including protected areas. This has led to decreasing numbers, population restructuring, and the loss of genetic diversity, as shown for pied tamarins (*Saguinus bicolor*), northern muriquis (*Brachyteles hypoxanthus*), Udzungwa red colobus monkeys (*Piliocolobus gordonorum*), several species of Chinese colobines (*Rhinopithecus* and *Trachypithecus*), Cross River gorillas (*G. gorilla diehli*), and Bornean orangutans (*39–45*). Edge effects predominate in many areas of disturbed forests, exacerbating habitat degradation (*37*). Agricultural expansion as well as legal and illegal logging cause further desiccation of vegetation, and human-induced forest fires devastate large areas in primate range regions yearly, resulting in increased tree mortality and losses of up to one-third of canopy cover (*46, 47*). Although the effects of habitat loss, fragmentation, and degradation upon primates are mediated by variations in species-specific traits (rarity, trophic levels, dispersal mode, reproductive biology, life history, diet, and ranging behavior), the common response across taxa is population decline (Fig. 1).

Some primates are more behaviorally and ecologically resilient than others when faced with habitat loss, fragmentation, and degradation. Bornean orangutans, for example, can survive, at least temporarily, in logged forests, *Acacia* plantations, and oil palm plantations (*48*). Baboons (*Papio*), Hanuman langurs (*Semnopithecus*), and macaques (*Macaca*) are particularly adaptable and can survive even in urban areas (*49*). Chimpanzees appear to evaluate risks when crop-foraging and adjust their foraging patterns in deciding whether to exploit fragmented forests near humans (*50*). Bonobos tend to avoid areas of high human activity, fragmented forests, or both, and although this may suggest flexibility, the presence of humans appears to significantly reduce their access to potentially available habitat (*51*). Still, persistence in isolated forest fragments, logged forests, agroecosystems, and urban areas is unlikely to be a sustainable option for most species due to hunting, further habitat reduction and fragmentation, reduced carrying capacity, parasite and disease transmission from humans and domestic animals, dog predation, human-primate conflict due to crop raiding, isolation, and continued changes in land use (*52*).

Primates in degraded forests face nutritional shortfalls and lower gut microbial diversity (*53–55*). They also show an increased prevalence of parasites and pathogens. For example, the increased exposure of lemurs (*Avahi laniger*, *Eulemur rubriventer*, *Hapalemur aureus*, *Microcebus rufus*, *Propithecus edwardsi*, and *Prolemur simus*) and chimpanzees (*P. troglodytes*) to human populations has increased their risk of infection by diarrhea-causing enteric pathogens (*56, 57*). The close phylogenetic relationship between humans and other primates also creates an exceptionally high potential for pathogen exchange (*58*), as evidenced by disease emergence in humans as an unintentional effect of the hunting and butchering of wild primates (for example, human outbreaks of Ebola and the global HIV/AIDS pandemic) (*59*). In addition, exponential human population growth (fig. S7, A and B) and associated human-induced forest loss increase opportunities for wild primates to become exposed to human and domesticated animal pathogens (*60*). Primates escaping or released from the pet trade or sanctuaries can carry pathogens with a potential of transmission to resident populations (*61*). Moreover, ecotourism and research, despite contributing in positive ways to primate conservation, have the unintended consequence of exposing wild primates to human pathogens (*62, 63*).

Hunting

Human population growth and increasing per capita wealth have led to an increase in commercialized bushmeat hunting relative to subsistence hunting in many parts of the world. This has become a major driving force for primate population decline, especially in Africa and Southeast Asia (*45, 64*). Although bushmeat hunting is difficult to track, reports indicate that about 150,000 primate carcasses from 16 species were traded annually as bushmeat in urban and rural markets at 89 sites in Nigeria and Cameroon (Supplementary Text) (*64*). In Borneo, between 1950 and 3100 orangutans are estimated to be killed annually (including 375 to 1550 females), a level that far exceeds the maximum sustainable offtake for population viability (*45*). Because only a relatively small number of primates live inside protected areas [for example, 21 to 27.5% of all great apes (*51, 65*)], populations outside protected areas are declining rapidly; the consequent increase in rarity raises the price of primate meat, making it more worthwhile for poachers to risk encroaching into protected areas to hunt (*66*).

Legal and illegal trade

Many primate species are increasingly threatened by legal and illegal unsustainable trade. Primates are traded for consumption, biomedical research, and zoo and wildlife collections; as pets; for the sale of body parts (bodies, skins, hair, and skulls) used in traditional medicine; as talismans and trophies; and for magical purposes (*67, 68*). The Convention on International Trade in Endangered Species (CITES) database for 2005–2014 reported a global primate trade of some 450,000 live individuals plus an additional 11,000 individuals in the form of body parts. Asian species accounted for 93% of this trade (12 genera), Neotropical species for 4% (13 genera), and African species for 3% (33 genera) (table S6 and fig. S8, A to C). However, these figures are conservative because CITES only reports statistics formally provided by each country. For example, although CITES reported fewer than 400 night monkeys (*Aotus*) traded internationally between 2005 and 2014 (table S6), in the tri-border area between Perú, Brazil, and Colombia, it was estimated that ~4000 night monkeys (*Aotus nancymaae*, *Aotus vociferans*, and *Aotus nigriceps*) were traded to a single biomedical research facility between 2007 and 2008 alone, for a price of approximately $100,000 (*69*). The expansion of road networks in frontier forests facilitates the extraction and trade of primates to cities and beyond borders (*25*). Together with increasing opportunities from e-commerce, this has given suppliers and smugglers unprecedented access to new markets *(70, 71*). Wildlife laundering (mixing protected species with legal shipments of similar species) also occurs when wild-collected primates are passed off as captive bred (Supplementary Text) (*72*).

Climate change

Although empirical evidence for the impact of climate change on primates is scarce, a recent global assessment suggests that numerous primates will experience changing climatic conditions during the 21st century, with the Amazon, the Atlantic Forest of Brazil, Central America, and East and Southeast Asia being considered hotspots of climate change–induced primate vulnerability (*73*). Primate taxa with limited geographic distributions and species characterized by slow life history traits (for example, late age at first reproduction and long interbirth intervals) are highly vulnerable to shifting ecological conditions and are likely to be most affected (*74, 75*). Although some species may cope with these changes either by migrating to more suitable conditions or by adapting in situ, dispersal or range shift is not always possible and may have highly negative consequences (Supplementary Text) (*76*). Forest fragmentation induced by climate change can affect the availability of dispersal routes (*77*). Climate change may also force individuals out of protected areas, making them more vulnerable to hunting and other anthropogenic impacts (*78*), and range shifts among interacting species can affect food supplies and introduce new predators, pathogens, and/or competitors (*79*). Interactions between climate change and other extinction drivers also need to be considered. For instance, projections of land-cover change show that the Bornean orangutan might lose 15 to 30% of its habitat by 2080, mainly due to deforestation and oil palm agriculture, but when coupled with climate change, even more habitat is likely to become unsuitable (*80*). Additionally, more frequent and severe climate change can induce floods, droughts, fires, hurricanes, and El Niño–Southern Oscillation events (81) that can affect the food supply available to primate populations, with negative impacts on health, fertility, and mortality (*82*).

Extinction risk and phylogenetic signal

The effect of anthropogenic threats on primates may be compounded by phylogenetic relatedness. Multispecies analyses have shown that extinction risk is not spread randomly across mammalian taxa. Rather, the prevalence of threatened taxa in some clades but not in others implies a strong phylogenetic pattern in susceptibility (*83, 84*). Our own comparative analysis of 340 primate species suggests that closely related species are more likely to face the same threat status relative to species selected randomly from the phylogeny (Fig. 5, fig. S9, A to C, and Supplementary Text). This result is likely due to the fact that related taxa share intrinsic aspects of their biology, such as body mass, life history, reproductive physiology, geographical distribution, dietary requirements, and behaviors (*85–87*). For example, several colobines (*Trachypithecus*, *Presbytis*, and *Simias*) in Southeast Asia are highly threatened island endemics and share biological traits known to increase their exposure and vulnerability to threats and extinction risks, such as relatively large body mass, diurnal behavior, and restricted geographic ranges.

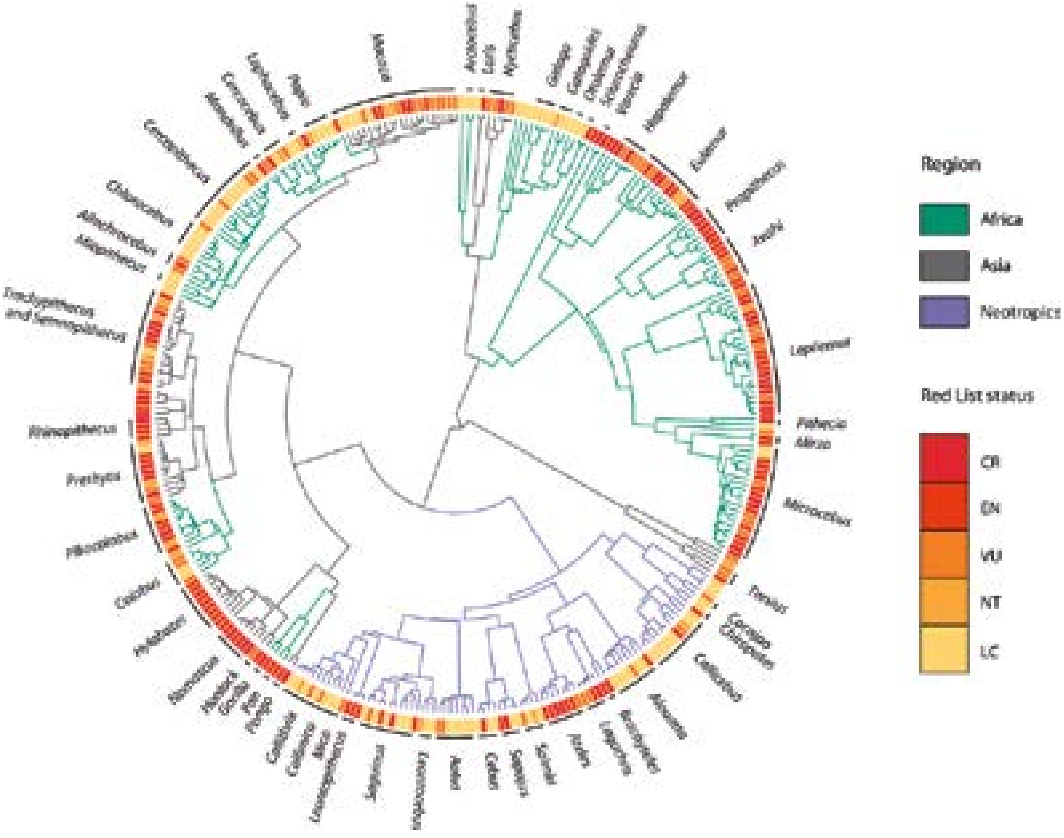

Fig.5. Phylogenetic signal as a predictor of extinction risk in the world's primates.

Distribution of threat values (IUCN Red List categories) for 340 primate species. Representative genera labeled. After taxonomic updates, our working phylogeny included 350 of the 367 species considered in the molecular supertree (*73*), of which 340 are not Data Deficient. Closely related species are more likely to have the same threat status than species taken randomly from the phylogeny [$D = 0.31$; $P(D < 1) < 0.001$], supporting a strong phylogenetic signal (see Supplementary Text for details of methodology). Data for Africa include Madagascar. IUCN Red List Categories: CR (Critically Endangered), EN (Endangered), VU (Vulnerable), NT (Near Threatened), and LC (Least Concern).

WHY PRIMATES MATTER

Social and cultural importance

Beyond sharing a close evolutionary history with humans, primates contribute importantly to the biological and cultural richness and the natural heritage of the countries in which they occur. Many primates play key roles in ecosystem dynamics and sustainability and are central figures in local and regional traditional knowledge, folklore, history, and even economies (*88*). For example, throughout South and Southeast Asia, monkeys figure strongly in Hindu and Buddhist mythology (for example, the Hanuman langur is the monkey god Hanuman in the Ramayana) and have centuries-old sympatric relationships with humans at temples and holy shrines. Today, many of these “monkey temples” are tourist sites, where the monkeys are protected, and provide an important source of income for local populations (*88*). Many traditional societies protect or tolerate primates and have integrated them into their historical narratives as sacred cultural figures and persons, as pets, and as food. For example, the Amazonian Guajá people integrate monkeys into their kinship and religious systems while also relying on primates as a sustainable food source (*89*). As primates become locally rare or extinct, we risk losing complex ecological, social, and cultural relationships that have developed between humans and primates over millennia (Supplementary Text) (*88, 90*).

Ecological importance

Primates are prey, predator, and mutualist species in food webs and thereby influence ecosystem structure, function, and resilience. Their evolution, feeding ecology, and geographic distribution are closely linked to the diversification of angiosperms, a principal source of food (pollen, nectar, fruits, and seeds) (*91*) for many animals and humans (*92–94*). Many primates have been identified or suspected as important pollinators due to their opportunistic nondestructive feeding on flowers and nectar (94, 95). As consumers of different plant parts (for example, fruits, flowers, seeds, gums, and leaves), primates can affect plant propagule dissemination, cause tree mortality, and may negatively affect the reproductive investment of some plants (*95*). However, numerous primates are highly frugivorous, and their relatively large size enables them to disperse small and large seeds over long distances, enhancing forest regeneration (*95*). In the absence of zoochorous seed dispersal by primates, plant populations can experience decreased genetic heterozygosity and increased genetic subpopulation differentiation, increased negative density dependence, and decreased recruitment (*96–99*). For example, Madagascar’s lemurs display complex relationships with large seed–producing trees, and lemur extinction may be facilitating a decline in the viability of certain Malagasy tree species (*100*). The population collapse of large atelids and cebids in heavily hunted forests of Amazonia has severely degraded long-term forest dynamics and the sustainability of many hardwood tree species with implications for the carbon-storing potential of forests (*101, 102*). Similarly, the hunting of gibbons in northern Thailand has had a negative effect on the demography of the lapsi tree (*Choerospondias axillaris*), which depends on gibbons to disperse its seeds into light gaps (*103*). The loss of primate seed dispersers has demonstrable impacts on human populations in the same ecosystems. For example, 48% of the plants whose seeds are dispersed by primates in the western regions of Côte d’Ivoire and 42% in Uganda have economic or cultural utility to local human inhabitants (*92*). In southern Nigeria, rural people rely on gathering primate-dispersed fruit and seed species (*104*), suggesting the considerable importance of primate conservation to local human food security.

Primates as model animals

Primates are highly valued model animals, advancing our understanding of the evolutionary history of our species and providing insight into human behavior, cognition, parenting, cooperation, adult social bonds, forms of social conflict and resolution, learning and memory, and the evolution of tool use and language (*105–108*). Although there exist important ethical issues that need to be considered when using primates in medical research (*109*), primate models have furthered our understanding of atherosclerosis, respiratory diseases, HIV/AIDS, treatment responses to psychoactive drugs, psychopathologies, sociality, mental health disorders, communication, immunology, brain functioning, pharmacology, endocrine regulation of reproduction, genetics and genomics, and disease risk and parasite dynamics, among many other subjects (*109*). Wild primate populations may hold valuable clues to the origins and evolution of important pathogens and processes of natural disease transmission by serving as sentinels for early disease detection, identification, and surveillance, thus benefiting humans. Because emerging infectious diseases also pose serious threats to both endangered and nonendangered primate species, studies of these diseases in one primate population may benefit conservation efforts for others (*59*).

ADDRESSING CONSERVATION NEEDS

Deforestation, hunting, illegal trade, and wood extraction are leading to a worldwide impoverishment of primate fauna. Drivers of primate loss are dynamic and interact with each other at local, regional, and global scales, leading to a trajectory of biosimplification that is most keenly felt as marked reductions in population sizes and, all too soon, extinctions (Fig. 6). The global scale of primate population declines and the predicted increase in the intensity of major anthropogenic threats (Fig. 1) suggest that conserving wild primates is an immediate but daunting challenge. Without widespread systemic changes in human behavior, populations will continue to decline over the next few decades, with species currently listed by the IUCN as Threatened becoming extinct and species now classified as Near Threatened or Least Concern facing increased extinction risk. Many primates are iconic (for example, gorillas, chimpanzees, orangutans, spider monkeys, and lemurs; Fig. 7), but given the scale of their decline, it is clear that neither their charisma nor their flagship status is sufficient to safeguard them from the threat of human-induced extirpation throughout their native ranges. Extinction rarely results from deficient scientific knowledge of the steps required to protect the species. Instead, it is embedded in political uncertainty, socioeconomic instability, organized criminality, corruption, and policies that favor short-term profits over long-term sustainability (*110*). Meaningful primate conservation will require a major revolution in commitment and policy. Alleviating pressures upon primate habitats requires decreasing the per capita demand of industrialized nations for tropical hardwoods, beef, palm oil, soy, rubber, minerals, and fossil fuels, among other goods, while simultaneously promoting sustainable resource-use practices (Fig. 6) (*111*).

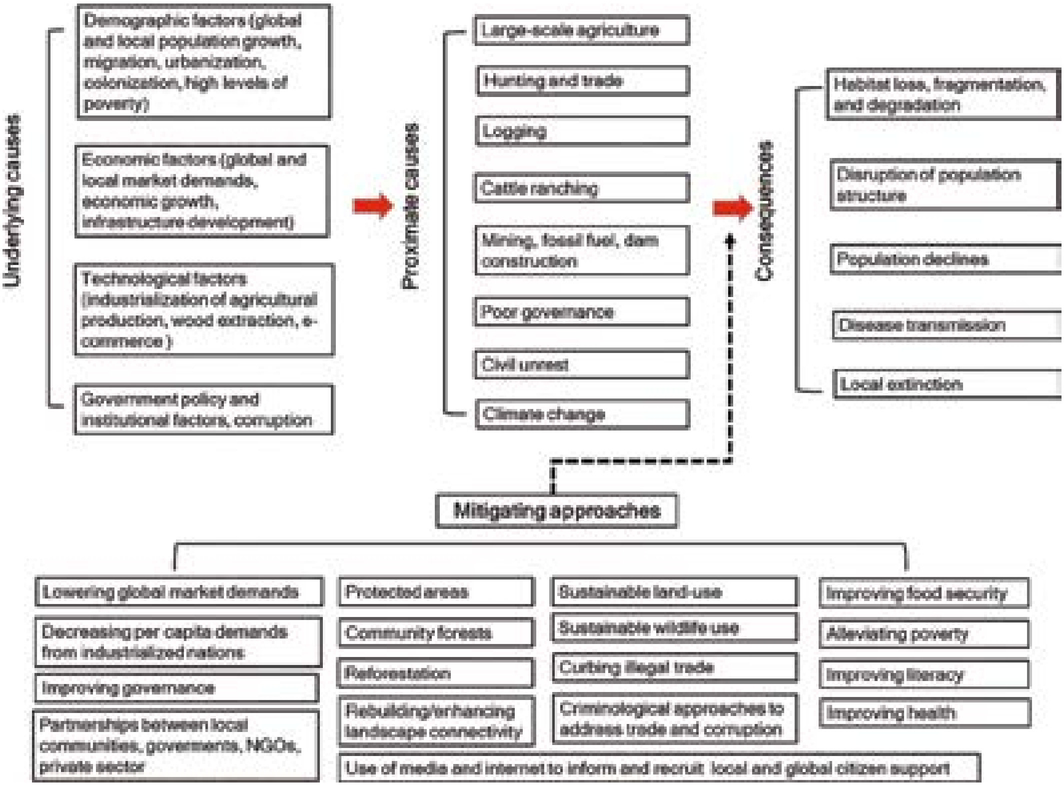

Fig.6. Factors driving primate population declines and possible mitigating approaches.

Four broad social and economic processes drive the proximate causes of threat to primates and human actions that directly affect primate habitats and populations. Mitigating approaches aim at lowering the impact of proximate causes of primate declines. Infrastructure development also includes road and rail expansion.

Fig.7. Photos of selected primates from each major world region.
Conservation status and photo credits include the following: (**A**) Golden snub-nosed monkey (*Rhinopithecus roxellana*), Endangered, P. A. Garber. (**B**) Ring-tailed lemur (*Lemur catta*), Endangered, R. A. Mittermeier. (**C**) Udzungwa red colobus (*P. gordonorum*), Endangered (Photo Credit: Thomas Struhsaker, Duke University). (**D**) Javan slow loris (*Nycticebus javanicus*), Critically Endangered (Photo Credit: Andrew Walmsley, Andrew Walmsley Photography). (**E**) Sumatran orangutan (*P. abelii*), Critically Endangered (Photo Credit: Perry van Duijnhoven). (**F**) Azara's night monkey (*Aotus azarae*), Least Concern [Photo Credit: Claudia Valeggia (Yale University)/Owl Monkey Project, Formosa-Argentina].

Improving the human condition

The human capital in primate range localities is of utmost importance to primate conservation. High rates of human population growth (5.1 billion people in 2010 to 7.3 billion in 2050 in primate range countries), high levels of poverty and inequality, the loss of natural capital due to extensive and rapid land-cover changes driven by global market demands, poor governance, and the need for food security, health, and literacy are key factors to consider (Supplementary Text and fig. S7, A to C). Solutions to the challenge of primate conservation must include reducing human birth rates and population growth, improving health, reducing poverty and gender biases in education, developing sustainable land-use initiatives, and preserving traditional livelihoods (Fig. 6) (*112*). Locally, people and governments need to become stakeholders in this effort and perceive that they can benefit from protecting primate populations and their forests while at the same time satisfying their basic needs. This will require education, rethinking, and investment from government, nongovernmental organizations (NGOs), and the private sector. There is no single solution to this global problem. Primate ecotourism may be an effective approach in some localities (for example, gorilla ecotourism in Rwanda, DRC, and Uganda) (*113*). In others, mini-livestock breeding may be a productive route to improve food security (*114*). Because bushmeat is an important source of food and income for inhabitants from poverty-ridden primate range countries, as well as an important aspect of indigenous culture, in some countries, nonprimate game ranching and game farming may contribute to food security and indirectly to primate conservation (*115*).

Expansion of protected areas

Although the percentage of the land surface devoted to protected areas has steadily increased in primate range countries (fig. S7D), highlighting protected areas as the only plausible conservation tool may contribute to local poverty by denying poor people power over and access to the natural resources that support their livelihoods (*116*). Protected areas must be sufficiently large and provide suitable primate habitats, and species of concern must be present in sufficient numbers within those areas (*117*). Unfortunately, countries in the Neotropics, Africa, and Asia are currently downgrading, downsizing, and degazetting protected areas due to growing industrial-scale natural resource extraction, and a significant number of protected areas are experiencing substantial deforestation (*118, 119*). Despite these trends, protected areas can and do provide long-term sanctuary for wildlife. For example, a study in the Udzungwa mountains of Tanzania showed that colobine primate populations were stable in the protected areas but declined severely in the unprotected forests (*120*). An 8-year study (2007–2014) using camera traps to annually monitor terrestrial mammals and birds in 15 protected areas in the Neotropics, Africa, and Southeast Asia showed strong evidence of stability and even increases in populations, including those of 23 primate species (19 cercopithecines in Africa and Asia, 3 African apes, and 1 lemur) (*121*). A complementary conservation approach is the REDD+ program, where payments are made to tropical countries to reduce emissions from deforestation and forest degradation (*122*). REDD+ could be a productive approach to increasing primate habitat and connectivity via reforestation and to providing important economic and ecological value for local populations. However, as of yet, no examples of implemented programs and their success on primate conservation are available (*123*).

Land-sharing and land-sparing

Because forests are among the few economic assets available to the rural poor in the tropics, securing their ownership and sustainable commercial use can help poor families cope with and move out of poverty (*124*). In a land-sharing approach (mixing protection and production in an agroecological matrix), community-managed forests are one option to integrate forest management into national poverty reduction programs in rural areas, favoring primate species with small area requirements. These forests also have lower and less variable annual deforestation rates than protected ones (*124*). In both land-sparing (favoring species with large area requirements) and land-sharing approaches, promoting biodiversity and the use of lattice-work corridors to connect landscapes along latitudinal and elevational gradients may promote a diversity of habitats for the long-term persistence of primate species that differ in their ecological requirements and may mitigate some of the deleterious effects of climate change (*125, 126*). A recent study of the fauna, including lemurs, of a 90-km-long biodiversity corridor connecting two national parks in Madagascar showed the need to differentiate among passive dispersers (species that settle randomly around the source population), active dispersers (species that settle only in favorable habitats), and gap-avoiding dispersers (species that avoid dispersing across nonhabitat areas). Thus, a better understanding of the natural history of different primates is critical to identify which taxa might be sustained within forested corridors and those for which no substitute or alternative habitat exists (*127*).

Use of new and traditional technology to monitor primate population vulnerability

A new science of monitoring primate habitats, population status, and anthropogenic threats is currently emerging. It includes taking advantage of global telecommunication systems and wireless Internet, satellite- and airborne-based imagery, drone technology, ever more powerful handheld devices (for example, smart phones and tablets), and camera traps (Supplementary Text) (*120, 128*). Combined with geographic information system and ground surveys, some of this technology has been used in evaluating sustainable land-use spatial planning and human-primate conflicts [for example, Javan gibbons (*Hylobates moloch*)] (*129*) and in providing case-by-case assessments of species vulnerability to climate change, as shown for Borneo's orangutans (Supplementary Text) (*80*). These same technologies can also be used by local citizen scientists for species and habitat monitoring, thus enhancing the effectiveness of mitigation measures (*128*). Recent technological advances in molecular biology—particularly high-throughput sequencing of DNA extracted from noninvasive samples (for example, feces, urine, and hair)—can accelerate assessments of population size and structure, genetic diversity and evidence of outbreeding, diet (plant, vertebrate, and invertebrate DNA consumption), and parasite and gut microbial diversity for wild primates (*130–134*). These advances have allowed researchers to identify species and origins of primate parts confiscated in the illegal bushmeat or pet trade (*135*) and are helpful in the genetic assessment and management of captive populations designed to establish viable, hybrid-free, "backup" populations to refresh the genetic pool of wild populations via reintroduction (*136, 137*).

Although these innovations open new avenues for primate study, successful, long-term programs that monitor primate population abundance also rely on simpler and less expensive methods that engage students and local research assistants, such as traditional census methods. There are relatively few multigeneration studies of primate population dynamics, largely because primates are long-living animals and population changes occur over time periods longer than the duration of most studies and research grants. However, a recent study from the Udzungwa Mountains of Tanzania combined locally based monitoring routines and advanced statistical approaches to investigate population abundance, even when information was missing for some monitoring periods (*120*). Another study showed the value of basic field procedures (transect surveys) in monitoring Sumatran orangutan populations, with results that doubled the estimated population from 6600 to 14,613, even though the population was still assessed as declining rapidly due to deforestation (*138*).

Mitigating illegal trade

It has been noted that to mitigate wildlife poaching, interventions need to go beyond regulation by encouraging capacity building in local communities to conserve wildlife, reexamining sustainable offtake mechanisms, such as regulated trade, ranching, and wildlife farming (*139*), and to use social media and the Internet to reduce demand and, ultimately, to curb trade (Supplementary Text and Fig. 6) (*71, 140*). Although the use of social media to raise local, regional, and global awareness of the plight of the world's primate fauna and of the ecological, social, cultural, and economic importance of primates is, no doubt, essential, it is just as important to develop local, action-oriented conservation education programs, especially those targeting young people and community decision makers. These are powerful conservation tools, combining knowledge and action acquired from successful ongoing programs in Madagascar (*141*), West Java, Indonesia (*142*), and Colombia (*143*) (see details in Supplementary Text). Criminological investigation that focuses on bushmeat trade and the trafficking of primates for pets, body parts, and trophies is also important for tracing the supply chains and criminal networks involved in illegal trade (see the "Focus of future research efforts" section).

Reintroductions and long-term forest protection as conservation tools

Where primate species are locally extinct, reintroductions are an option but can be expensive, and long-term protection of forests is arguably a more cost-effective means of preserving primates than reintroduction (*144*). Nonetheless, reintroductions raise public and political awareness and provide placement solutions for rescued animals in line with welfare concerns. The use of wild-born, rescued, and rehabilitated primates instead of captive-bred animals in reintroduction programs reduces costs and can increase success (*145*). A range of primate species have been successfully introduced in some places, including orangutans, lar gibbons (*Hylobates lar*), southern yellow-cheeked gibbons (*Nomascus gabriellae*), Indonesian slow lorises (*Nycticebus*), Delacour's langurs (*Trachypithecus delacouri*), western gorillas, woolly monkeys (*Lagothrix lagotricha*), golden lion tamarins (*Leontopithecus rosalia*), and pygmy marmosets (*Cebuella pygmaea*) (*146–150*). Still, evidence of outbreeding and introgression in, for example, Bornean orangutan populations due to the reintroduction of rescued animals of different species and subspecies into wild populations highlights the care that must be taken using these kinds of conservation interventions (*151*).

Reducing the urban footprint on primate habitats

Worldwide, urban policies need to be targeted at reducing people's ecological footprints in primate range regions. For instance, promoting the recycling of cell phones, laptops, and other electronic devices could diminish the demand for coltan mining from the Congo Basin in Central Africa, which threatens primates in the region, including gorillas and chimpanzees (*22, 152*). Decreasing the world's per capita demand for tropical hardwoods, food and nonfood products, minerals, and fossil fuels, among other goods, from primate range regions would help alleviate pressures on primate habitats (*112*).

FOCUS OF FUTURE RESEARCH EFFORTS

The scientific research effort on primates, as measured by the number of published articles on individual primate species on the Web of Science from January 1965 to March 2016, yielded ~47,000 records pertaining to both wild and captive primates. Overall, 16% involve studies of Neotropical monkeys, 36% of African primates, and 48% of Asian primates. Sixty-six percent of the publication records focused on a single family, the Cercopithecidae, principally Macaca in Asia and *Papio* in Africa (fig. S10). These results reflect the important role of some taxa in this family (for example, *Macaca mulatta* and *Papio anubis*) as models for studies of human health, behavior, and physiology. Studies of primates in the African Hominidae (chimpanzees, bonobos, and gorillas) constituted another 10% of the total records, and species in the Neotropical families Callitrichidae, Cebidae, and Atelidae combined constituted 13%. Species in the remaining 11 primate families accounted for only 11% of the total records (fig. S10). Thus, despite considerable research efforts over the past 40 years, scientific data for a great majority of primate species are still limited. Moreover, decade-long studies have been conducted on very few species, and studies spanning several generations are even fewer. Such paucity of knowledge suggests that there is an urgent need to generate species- and habitat-specific knowledge about population size, life history and ecology, habitat loss, forest fragmentation, climate change, potential for disease transmission, and human-primate interactions, including detailed population/species recovery plans.

Cultural mapping and the fostering of mutually beneficial partnerships with government and people in local communities, coupled with ethnoprimatological field work, are effective tools to identify specific problems and workable in situ solutions for primate conservation (*153*). For example, a decade-long study in the Central African Republic revealed that traditional forest uses (for example, hunting and gathering) have been replaced by new activities, such as logging, bushmeat hunting, and even conservation programs, and that local human populations are both materially and culturally impoverished by animal declines (*153*). Another study showed that the use of lorises (*Nycticebus* and *Loris*) in traditional medicine and the pet trade in Sri Lanka, Cambodia, and Indonesia followed culturally specific patterns (*154*), and therefore, a deep understanding of local customs is required to develop effective conservation policies.

Because the unprecedented market globalization of the illegal wildlife, bushmeat, and amulet trade is rapidly depleting natural primate populations (*110*), criminological intelligence network analyses, within and outside range states, is critically needed. To be effective, this effort needs to integrate local and global attitudes about environmental insecurity and biodiversity exploitation. For example, local people's perceptions of the risk associated with illegal lemur hunting in Madagascar do not reflect the perception of policy makers (*155*). Attention to poaching as a serious conservation crime will yield a better understanding of whether local people engage in such activities to ensure food security and/or to generate income and may illuminate how best to incentivize sustainable alternatives, such as food subsidies or employment as rangers and conservation guards (*156*). Given the severity of this problem, the social and organized crime contexts of primate bushmeat and live trade need to be included in an integrated model (*157*) that also addresses corruption in supervising government entities in charge of monitoring and prosecuting illegal trade (Fig. 6) (*110*).

Finally, studies that document the interactions of anthropogenic drivers of environmental change with species-specific biological and behavioral traits (for example, body mass, reproductive rate, dietary flexibility, and nutritional needs) within a phylogenetic comparative framework are needed to further our understanding of the imminent threats faced by individual taxa, especially for species that have few close taxonomic relatives. Over the past two decades, a resynthesis and reorganization of new and previously collected data have increased the number of recognized primate species from 180 to 376 in 2005 and from 376 to 504 in 2016 (*158–161*). The recognition of the urgent need to understand the diversity of threatened primates inspired a workshop in 2000 in Orlando, Florida, sponsored by Disney's Animal Kingdom. This workshop gave rise to landmark conservation assessments and action plans for each of the major primate regions (*162–166*).

CONCLUDING COMMENTS

Despite the impending extinction facing many of the world's primates, we remain adamant that primate conservation is not yet a lost cause, and we are optimistic that the environmental and anthropogenic pressures leading to population declines can still be reversed. However, this is contingent on implementing effective scientific, political, and management decisions immediately. Unless we act, human-induced environmental threats in primate range regions will result in a continued and accelerated reduction in primate biodiversity. Primate taxa will be lost through a combination of habitat loss and degradation, population isolation in fragmented landscapes, population extirpation by hunting and trapping, and rapid population decline due to human and domestic animal-borne diseases, increasing human encroachment, and climate change. Perhaps the starkest conclusion of this review is that collectively - as researchers, educators, administrators, and politicians - we are failing to preserve primate species and their habitats. We face a formidable challenge moving forward, as success requires that sustainable solutions address the social, cultural, economic, and ecological interdependencies that are the basis of primate conservation. Our review suggests that by refocusing and publicizing our efforts to academics, government agencies, NGOs, businesses, and the public at large, we can build a comprehensive understanding of the consequences of primate population declines and encourage urgent and effective conservation policies. These policies will differ among countries, regions, habitats, and primate species based on the site-specific nature of each problem. We have one last opportunity to greatly reduce or even eliminate the human threats to primates and their habitats, to guide conservation efforts, and to raise worldwide awareness of their predicament. Primates are critically important to humanity. After all, they are our closest living biological relatives.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/3/1/e1600946/DC1

fig. S1. Primate habitat countries ranked by the number of species present.

fig. S2. Countries with primate species in the Neotropics, Africa (including Madagascar), and Asia and percent of countries with threatened species.

fig. S3. IUCN threat categories and population status of primate species.

fig. S4. Percent of primate species listed under each proximate threat, according to the IUCN.

fig. S5. Growth trends in cattle stock, agricultural activity, and deforestation in primate range regions.

fig. S6. Agricultural expansion and declines in forest cover for the period 1990–2010 in the Neotropics, Africa, and Asia.

fig. S7. Human population growth in primate range regions.

fig. S8. Global primate trade for the period 2005–2014, as reported by parties to the CITES Secretariat.

fig. S9. Phylogenetic patterns associated with extinction risk for primate species in the Neotropics, Africa, and Asia.

fig. S10. Number of published articles found in the Web of Science for primate species in each family.

table S1. Primate species in the Neotropics grouped by family.

table S2. Primate species in mainland Africa grouped by family.

table S3. Primate species in Madagascar grouped by family.

table S4. Primate species in Asia grouped by family.

table S5. Summary of sources of threat and the number of primate species affected, according to the IUCN Red List.

table S6. Global international trade in primates for the period 2005–2014, as reported by parties to the CITES Secretariat.

Supplementary Text

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Impending extinction crisis of the world's primates – Implications for Vietnam

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Key words: deforestation, forest fragmentation, protected areas, poaching, hunting, primate trade, conservation needs, law enforcement, captive breeding, reintroduction

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Summary

The article "Impending extinction crisis of the world's primates: Why primates matter" (Estrada et al. 2017 and as reprint on page 1 to 24 in this issue) provides an overview about the dramatic situation of nonhuman primates worldwide. Vietnam is among the top priority countries with one of the highest numbers of threatened primate species. With a total of 25 taxa, Vietnam exhibits the largest primate diversity of all countries on the Southeast Asian mainland. More than 90% of these taxa are threatened with extinction, which indicates the dramatic situation. Following the factors that impact primate populations and as discussed by Estrada et al. (2017), key points for primate conservation in Vietnam should be specified and their significance assessed.

With 2.27 million ha of protected area, which makes 6.8% of the countries land territory, Vietnam provides relatively good conditions for the protection of natural resources including fauna and flora. However, deforestation of natural forests in Vietnam is proceeding at an alarming rate, and even though forested areas in general increase through reforestation it is predominantly as monoculture plantations. Furthermore, a large number of protected areas are very small or fragmented, and are therefore highly vulnerable to anthropogenic impacts. In many cases, adjacent unprotected areas possess the same habitat, but are reserved for different usage, often without any detailed management. In Vietnam, some 25 million people depend on forests for subsistence and livelihoods, including wages, which affects a variety of species used for non-timber forest products, as well as species that are logged or used as fuel wood. Despite the dwindling forest areas and the decreasing quality of natural forest, there is currently enough adequate habitat for Vietnamese primates, but fragmentation exhibits a long-term threat for most of the species.

The biggest threat to all primate species in Vietnam is poaching. The legal primate trade in Vietnam is restricted to the import and export of macaques for biomedical research, and there are several farms in Vietnam that breed macaques for this purpose. However, laundering wild-caught macaques through breeding farms is common. For instance, wild-caught long-tailed macaques have been illegally exported from Cambodia to Lao PDR where they have been illegally re-exported to Vietnam for use in breeding farms; occasionally with forged CITES permits. Primate poaching is widespread and common, but it is not the result of subsistence among locals and those of lower socioeconomic status in Vietnam. Rather, poaching provides additional income to improve living standards. Forest rangers and other institutions responsible for the protection of the country's forested areas lacks training, education and the right to enforce laws. The power of forest rangers is limited and they lack an equivalent authority as the police. Equipment and funds for effective protection work are also insufficient. Law enforcement is the most critical point for effective protection in Vietnam. The essential reason for the immense volume of wildlife in the illegal trade and the dramatic decline of wild animal populations - not only primates – results from an ineffective, unmotivated and apathetic enforcement of existing laws. Since decades, hundreds of reports on wildlife, wildlife trade, programs and regulations call for immediate and strong law enforcement, with minimal impacts on practice. Internet and social media have also been used for illegal wildlife trade.

Vietnam is among the countries most adversely affected by climate change, but its impact on primate populations remains speculative. More immediate and direct impacts to the abundance and distribution of primates in Vietnam are land cover changes, habitat fragmentation, and poaching. The long-term survival of a species depends on the survival of a viable population in an intact wild habitat. However, for many of Vietnam's primate species their survival in the wild cannot be guaranteed. Captive breeding and reintroduction are costly conservation interventions, but should be considered if preservation in the wild is impracticable or unsuccessful. With the high number of primate species threatened with extinction, various conservation interventions such as extension of existing protected areas, strict law enforcement, and captive breeding management are urgently required to prevent the loss of diversity and species.

Sắp xảy ra cuộc khủng hoảng tuyệt chủng các loài linh trưởng trên thế giới: Những gợi ý cho Việt Nam

Tóm tắt

Bài báo tổng hợp "Khủng hoảng tuyệt chủng thú linh trưởng trên thế giới: Tại sao lại là các loài linh trưởng" đã cho cái nhìn tổng quan về tình hình đáng lo ngại của linh trưởng trên thế giới. Trong đó, Việt Nam là nước cần ưu tiên hàng đầu vì có nhiều loài linh trưởng nguy cấp nhất. Với tổng số 25 loài và phân loài, Việt Nam có mức độ đa dạng thú linh trưởng lớn nhất vùng lục địa Đông Nam Á. Tuy nhiên đáng buồn là có hơn 90% số loài đang bị đe dọa tuyệt chủng. Những yếu tố ảnh hưởng đến quần thể linh trưởng đã được phân tích (Estrada và cộng sự 2017). Những điểm mấu chốt cho bảo tồn linh trưởng ở Việt Nam cần được nhận diện và đánh giá nghiêm túc. Với khoảng 2,27 triệu ha rừng thuộc các khu bảo tồn (chiếm 6,8% lãnh thổ), Việt Nam có các điều kiện tương đối tốt cho việc bảo vệ tài nguyên thiên nhiên, bao gồm cả động vật và thực vật. Tuy nhiên, nạn phá rừng tự nhiên ở Việt Nam đang diễn ra với một tốc độ báo động. Mặc dù tổng diện tích rừng tăng thông qua công tác trồng rừng, nhưng không may chủ yếu lại là rừng thuần loài.

Hơn nữa, phần lớn các khu bảo tồn có diện tích nhỏ đến rất nhỏ, dễ bị tác động. Các khu vực bảo vệ liền nhau có môi trường rừng giống nhau, nhưng có quy chế khác nhau. Đa phần không có bất kỳ kế hoạch quản lý chi tiết nào.

Ở Việt Nam, khoảng 25 triệu người sống phụ thuộc vào rừng. Điều này ảnh hưởng đến một loạt các lâm sản ngoài gỗ, gỗ nhiên liệu và khai thác gỗ. Mặc dù diện tích rừng tự nhiên đang bị thu hẹp và chất lượng giảm, điệu kiện hiện nay môi trường sống vẫn còn thích hợp cho các loài linh trưởng. Nhưng sự chia cắt của các sinh cảnh này tạo ra mối đe dọa lâu dài đối với hầu hết các loài.

Đe dọa lớn nhất đối với tất cả các loài linh trưởng ở Việt Nam là nạn săn trộm. Việc buôn bán linh trưởng hợp pháp ở Việt Nam thực sự là chỉ giới hạn trong việc nhập khẩu và xuất khẩu các loài khỉ cho mục đích nghiên cứu y sinh học. Có một số trang trại ở Việt nam giữ và nuôi khỉ giống cho mục đích này. Tuy nhiên, nạn buôn lậu khỉ hoang dã thông qua các trang trại chăn nuôi là phổ biến. Ví dụ, loài M. fascicularis hoang dã được xuất khẩu bất hợp pháp từ Campuchia sang Lào và từ đây đã xuất khẩu trái phép vào Việt Nam để sử dụng trong các trang trại chăn nuôi; đôi khi có giả mạo giấy phép CITES.

Nạn săn bắn linh trưởng vẫn phổ biến. Tuy không quá quan trọng đối với sinh hoạt phí cho người dân địa phương và người nghèo ở Việt Nam, nhưng là một cách tạo thêm thu nhập để cải thiện đời sống của họ. Lực lượng kiểm lâm có trách nhiệm bảo vệ các khu rừng thiếu đào tạo, giáo dục và quyền thực thi pháp luật. Sức mạnh của lực lượng kiểm lâm còn hạn chế và không có thực quyền như công an. Trang thiết bị và kinh phí không đủ cho công việc bảo vệ hiệu quả. Thực thi pháp luật thực sự là điểm tử huyệt tại Việt Nam. Lý do chính dẫn đến buôn bán động vật hoang dã bất hợp pháp và sự suy giảm đáng kể các loài động vật hoang dã, không chỉ các loài linh trưởng, đều do thực thi pháp luật rất kém hiệu quả, và sự thờ ơ. Hàng chục năm nay đã có hàng trăm báo cáo của các cuộc điều tra về động vật hoang dã, buôn bán ĐVHD, các chương trình và các quy định. Tất cả đều đã yêu cầu thực thi pháp luật ngay lập tức và mạnh mẽ hơn. Nhưng thực hiện vẫn còn xa mới đạt yêu cầu. Việc sử dụng phương tiện truyền thông Internet và mạng xã hội tiếp tục góp phần làm gia tăng buôn bán động vật hoang dã bất hợp pháp.

Việt Nam có thể sẽ là một trong những nước bị ảnh hưởng xấu nhất của biến đổi khí hậu, nhưng tác động của nó lên các quần thể linh trưởng vẫn chỉ có tính suy đoán. Tác động quan trọng và trực

tiếp hơn đến sự phân bố, độ phong phú của các loài linh trưởng ở Việt Nam là do sự suy giảm che phủ rừng, chia cắt sinh cảnh và nạn săn trộm. Sự tồn tại lâu dài của một loài hoàn toàn phụ thuộc vào sự tồn tại của một quần thể vững mạnh có sống hoang dã còn nguyên vẹn.

Đối với một số loài linh trưởng của Việt nam, sự tồn tại trong tự nhiên có thể không được đảm bảo. Vì vậy, nhân nuôi sinh sản và tái thả là những can thiệp nên được phối hợp và dự tính nếu bảo quản trong môi trường hoang dã hiện nay là không khả thi hay không thành công. Ở Việt nam, số lượng lớn các loài linh trưởng bị đe dọa và gần tuyệt chủng, các can thiệp bảo tồn khác chẳng hạn như việc mở rộng khu bảo tồn hiện có, thực thi pháp luật nghiêm ngặt và quản lý nuôi sinh sản, được yêu cầu cấp bách để ngăn chặn sự mất mát của các loài.

Introduction

The article "Impending extinction crisis of the world's primates: Why primates matter" (Estrada et al. 2017 and as reprint page 1 to 24 in this issue) provides an overview about the dramatic situation of the conservation status of nonhuman primates worldwide. The factors that threaten primate populations are comprehensively discussed and analysed, with examples to illustrate the impact on populations and species. Threats differ tremendously for species and between regions, and thus to develop recommendations and actions to ensure the survival of a certain species, an assessment of the local situation is required.

Vietnam is among the top priority countries with one of the highest number of threatened primate species. With a total of 25 taxa, Vietnam exhibits the largest primate diversity of all countries on the Southeast Asian mainland. More than 90% of these taxa are threatened with extinction, which indicates the dramatic situation compared to the assessment of primate families worldwide (Fig. 1). For many years, five Vietnamese primate species have been continuously listed on the "25 World's Most Endangered Primates (Conservation International, 2002; Mittermeier et al., 2000; 2005; 2007; 2009; 2012; Schwitzer et al., 2014; 2015), which accounts for 20% of the world's primates that are closest to extinction.

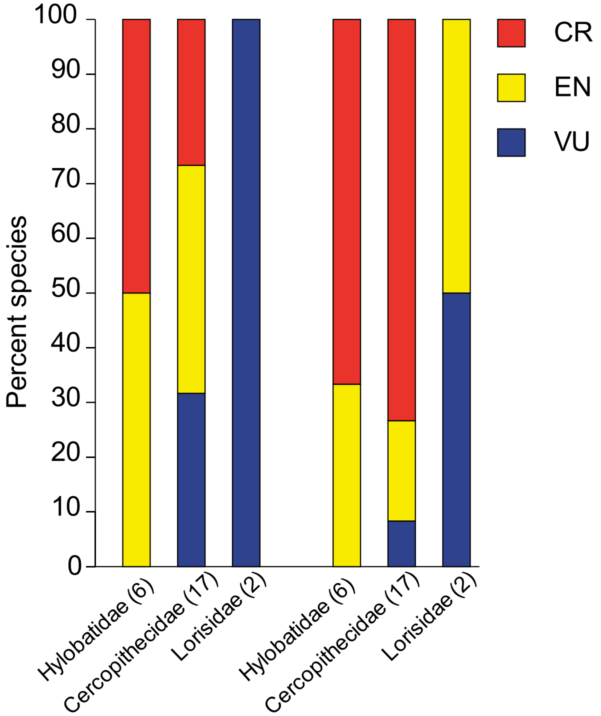

Fig.1. Percent of Vietnamese primate species threatened with extinction in each primate family (VU: Vulnerable, EN: Endangered, CR: Critically Endangered). In the left and right columns, the conservation status for global and only Vietnamese primate populations is shown. Numbers in parentheses indicate the number of Vietnamese species recognized in each family.

1. Factors threatening primate populations in Vietnam

Following a review of the factors that threaten primate populations, also discussed by Estrada et al. (2017), key points for primate conservation in Vietnam are specified and their significance assessed.

1.1. Land cover changes, deforestation and conversion of forest land

During war times (1945-1954 and 1961-1975), nearly 2 million ha of Vietnam's forest were lost. Since then, forest cover has further diminished substantially – in quantity and quality. Between 1980 and 1990 the country lost an average of 100.000 ha forest annually. By 1990, only 9,175 million ha (27.8% of the total land area) remained forested, including 745,000 ha plantations (Forest Science Institute of Vietnam, 2009). To counteract deforestation, the government implemented several reforestation programs and Vietnam's forest area has increased continuously since 1995 through forest plantation establishment and natural forest rehabilitation (Luong Thi Hoan, 2014). By 2009, Vietnam had 13.38 million ha of forest area (39.5% of the total land area) (Ministry of Agriculture and Rural Development, 2011). This increase in forest can be partially explained by increased plantations and the natural regeneration of forests, but it is also due to the re-categorization and inclusion of previously excluded limestone forest in the broader category of forest (Pham Thu Thuy et al., 2012). In contrast, the total area of natural primary forest continuously declined and lowland natural forest is almost entirely gone. Currently only about 80,000 ha of primary natural forest remains and even these are under threat (RECOFTC, 2011). At present, the deforestation of natural forests is proceeding at an alarming rate. Although reforestation has resulted in an increased forest area, most of that area consists of monoculture plantations, and meanwhile forest fragmentation and degradation of natural forests continues (Mayfroidt & Lambin, 2008). Values of forest coverage, forest growth, and loss differ by source because there is no conformity of definition to the terms primary forest, natural forest, regenerated forest and plantation. FAO (2016) mention that the area of naturally regenerated forest has increased steadily from 8.0 million ha in 1990 to 11.0 million ha in 2015. The area of planted forest also increased, from 0.97 million ha in 1990 to 3.66 million ha in 2015; this includes rubber plantations, which extended from 0.22 million ha in 1990 to 0.91 million ha in 2012. However, the increase of rubber plantations resulted in natural forest loss.

Land conversion is considered a primary driver for deforestation. According to satellite images, forest cover in the Central Highland, the area with the largest remaining contiguous forest in Vietnam, was reduced from 2.98 million ha in 2006 to 2.66 million ha in 2011 (Vietnam Heritage Magazine, 2013). From 2010 to 2015, forest cover in the Central Highlands fell almost 6%, or over 300,000 ha (Viet Nam News, 2016a). Despite an order of the Prime Minister in June 2016 to close natural forestes in the Central Highlands (VN Express, 2016; VN Net 2016) (Fig. 2) the illegal logging continues, occasionally supported by provincial leaders and administrations, e.g. the clearance of more than 500 ha forest in Binh Phuoc Province in 2016 (Viet Nam News, 2017) (Fig. 3). The dimension of illegal logging leads occasionally to drastic measures (Fig. 4).

Most of this conversion is the result of farmland extension and illegal logging. Worldwide, 80% of deforestation is driven by agriculture (The World Bank, 2016). The area for industrial crop production, such as coffee, rubber, cashew and pepper has increased considerably. Likewise, the construction of numerous hydro-power dams resulted in habitat destruction.

Primates are more frequently found only in protected areas such as national parks and nature reserves. These areas comprise 2.27 million ha (Nguyen Quoc Dung, 2014). However, tree cover in these areas make up only about 80%, while the remaining 20% is composed of shrub, grassland and bare land (Forest Science Institute of Vietnam, 2009).

Despite the dwindling forest areas and the decreasing quality of natural forest, there is still enough adequate habitat for Vietnamese primates. Four Vietnamese langur species that belong to the "limestone langurs" (*Trachypithecus delacouri, T. poliocephalus, T. francoisi, T. hatinhensis*) are restricted to areas with limestone outcrops and scattered limestone forest (Nadler & Brockman, 2014). This habitat is not under pressure through conversion into agricultural land or plantations, but through increasing limestone quarrying to cover the high demand of cement production.

Fig.2. At a conference to seek solutions to achieving sustainable forest recovery in order to cope with climate change in the Central Highlands, Prime Minister Nguyen Xuan Phuc ordered the closing of natural forests to save forests in the region from current degradation. Photo: Thong Nhat/VNA.

Fig.3. Protection forests in Kon Tum are destroyed to make room for cultivation. Photo: Quang Thai/VNA.

Fig.4. Staff at the Reservation Centre for the 'Critically Endangered' Chinese swamp cypress (*Glyptostrobus pensilis*) in Ea Ral Commune, Ea H'leo District, Dak Lak Province fortify barbed wire fences to protect forests. Photo: Duong Giang/VNA.

1.2. Forest fragmentation

Even if forest destruction can be stopped, fragmentation of forests remains a long-term threat to most primate species in Vietnam. Larger and viable populations require conservation intervention if the genetic diversity of fragmented populations is to be preserved. Smaller populations are very sensitive and vulnerable to several impacts, and poaching can wipe out whole populations quickly. As an example, surveys confirmed 19 isolated populations of the “Critically Endangered” and endemic Delacour’s langur (*T. delacouri*) in the 1990s. Between 2000 and 2010, ten populations were eradicated by poaching (Nadler, 2015).

Connecting fragmented and isolated forest areas and primate populations via the establishment of corridors is often unrealistic, particularly when the distance between areas, the complicated and lengthy land clearance procedures and the generally high human population density is considered.

1.3. Hunting

Hunting is the primary threat to all primate species in Vietnam (Fig. 5). Depending on species, they are hunted either for food, for the preparation of traditional medicine, and/or for the pet trade. Although Vietnam has a large forest ranger force for protection of the forests, motivation, training and education of the ranger staff is rudimentary. Equipment and funds for effective protection work are insufficient. Negligence and corruption lead to pervasive poaching and a growing illegal wildlife trade. The protection of a number of isolated populations, distributed occasionally in unprotected forest areas, is not manageable.

Fig.5. Hunted Delacour’s langur, a ‘Critically Endangered’ species, endemic to Vietnam and belongs to the ‘World’s 25 Most Endangered Primates’ with a total population of about 200 to 250 individuals. Photo: Tilo Nadler.

Palpable and effectual prosecutions are an exception. However, studies on primate hunting and trading based on records over 6 years shows a frustrating result. During this time (2008 to 2013) 1,079 violations were registered with 2,916 primates: lorises, macaques, langurs and gibbons. In average, 486 primates per year were recorded in the illegal trade, although these are only the registered cases. The number of unrecorded cases is undoubtedly much higher. Regardless, it can be estimated that more than one primate per day is illegally traded, which has extremely negative impacts on wild populations. The situation becomes extreme in light of the prosecution for violation of the law (Table 1). Imposed prison sentences are mostly suspended, thus, punishment is actually non-existent and is not a deterrent (Beyle et al., 2014).

Table 1. Prosecution for violations against the Vietnamese wildlife protection law, differenciated for the four in Vietnam distributed primate groups: lorises, macaques, langurs and gibbons. "No punishment" means there was evidence about violation but prosecution relinquished. "No findings" means it was no evidence anymore, because the primates, the hunter or trader disappeared.

Prosecution	Lorises	Macaques	Langurs	Gibbons	Average
1.No punishment	81%	78%	73%	60%	73%
2.No findings	15%	14%	9%	19%	14%
1. + 2.	96%	92%	82%	79%	87%
3.Fined	2%	8%	5%	15%	7%
4.Imprisonment	2%	0%	13%	6%	6%

1.4. Legal and illegal trade

Legal primate trade in Vietnam is only restricted to the import and export of macaques for biomedical research, and there are several farms that keep and breed macaques for this purpose. A wildlife farm census in only 12 provinces in southern Vietnam documented 4,099 operating wildlife farms and collected updated information on 1,218,547 kept individuals of 182 species. Additionally, there were 1,907 non-operational farms recorded holding 158,093 animals belonging to 45 wildlife species (FAO, 2014).

The most common species in these farms are oriental rat-snakes, crocodiles, tortoises, pythons, and various mammals (porcupines, palm civets, deer, wild boars, tigers, bears, and primates). The most common primate species is the long-tailed macaque (*Macaca fascicularis*). In southern Vietnam there is the world's largest captive-breeding primate facility with about 30,000 long-tailed macaques. Vietnam exported 21,681 live *M. fascicularis* between 1999 and 2003, and 40,198 between 2004 and 2008. Since 2004, Vietnam has imported 18,405 individuals from Laos, Cambodia and Myanmar. 4,400 of which were re-exported to China (Species Survival Network, 2010).

A report on illegal trade points to a sophisticated trans-border wildlife trafficking network involving wild-caught long-tailed macaques smuggled from Cambodia to Vietnam with forged CITES permits. Studies published in 2008 and 2010 reported that wild-caught *M. fascicularis* were illegally exported from Cambodia to Lao PDR, and then they were illegally re-exported to Vietnam for use in breeding farms (Mueller & Khy Sovuthy, 2015). Evidence gathered in 2015 points to the existence of a widespread illegal cross-border trade in wild *M. fascicularis* captured in Cambodia and transported to Vietnam. Field research has given rise to some serious concerns regarding the misuse of source CITES-codes by key *M. fascicularis* exporting countries. Research has revealed that countries may be declaring the source of *M. fascicularis* on CITES export and re-export permits as 'captive bred' or 'captive born', when they are in fact wild-caught (Hoang Quoc Dung, 2008; Mueller & Khy Sovuthy, 2015; Species Survival Network Primate Working Group, 2015). Concern about declining populations and a rapid expansion of trade in *M. fascicularis* has been expressed (Eudey, 2008) and during the International Primatological Society XXIII Congress in 2010, it was announced that the IUCN Species Survival Commission (IUCN/SSC) Primate Specialist Group will re-assess the conservation status of *M. fascicularis*.

The illegal trade in primate species not involved in captive breeding programs for laboratory use is difficult to assess, but continues in high numbers (see 1.3 above) (Fig. 6). According to estimates, the quantity of wildlife provided for the Vietnam market is about 3,400 tons per year (Nguyen Manh Ha et al., 2008), in which the quantity of illegal exploitation is ca. 18% (Do Kim Chung et al., 2003). According to the assessment provided by the Government, law enforcement has controlled only 5 to 10% of the total illegal wildlife trade (Government of Vietnam, 2004). Recent trends in the use of Internet and social media has helped to increase the illegal wildlife trade (Education for Nature-Vietnam, 2016; 2017), even though the CITES authority of Vietnam has attempted to prevent wildlife trafficking via the Internet in 2004 (Viet Nam News, 2013b). In 2008, the Wildlife Crime Unit (WCU) of Education for Nature – Vietnam recorded the first illegal online wildlife advertisement and as of June 2016, a total of 2,028 similar violations have been uncovered (Education for Nature-Vietnam, 2016).

Fig.6. A ‘Critically Endangered’ grey-shanked douc langur confiscated from the illegal primate trade. Photo: Tilo Nadler.

The press release to the “International Conference on Illegal Wildlife Trade” in Hanoi, November 2016 stated that the demand for illegal wildlife products has risen sharply in the last decade. The Vice State President of Vietnam remarked “Along with the commitments and statements, to ensure their sustainability we need to turn the commitments into practical field actions and create a mechanism to oversee the enforcement of these actions” (The Hanoi Conference on Illegal Wildlife Trade, 2016)

1.5. Climate change

Vietnam is among the countries that will be most adversely affected by climate change. During the last 50 years, Vietnam’s annual average temperature has increased by 0.5 - 0.7^{0}C, while the sea level along its coastline has risen by approximately 20 cm (Institute of Strategy and Policy on Natural Resources and Environment, 2009). Despite this presage scenario, the impact on primate populations in Vietnam remains speculative. More immediate and direct impacts to the abundance and distribution of primates in Vietnam are land cover changes, habitat fragmentation, and poaching.

2. Addressing conservation needs

With the high number of primate species threatened with extinction, conservation interventions are urgently needed to prevent the loss of diversity and species.

2.1. Improving human conditions

Worldwide, about 1.3 billion people – one-fifth of the global population – depend on forests for employment, forest products, and contributions to livelihoods and incomes. In Vietnam, some 25 million people depend on the forests for subsistence and livelihoods, including wages (The World Bank, 2016). This affects a variety of species used for non-timber forest products, as well as species that are logged or used as fuel wood. Primate poaching is widespread and common, but it is not the result of subsistence needs among locals and those of lower socioeconomic status. Rather, poaching provides additional income to improve living standards. Documentation from the Endangered Primate Rescue Center (EPRC) from over 200 confiscations show that in most cases the poacher brought the animals to a trader with the expressed plan to buy a new TV, rebuilt his house, and/or to support the marriage of his children (EPRC, unpublished). Points discussed by Estrada et al. (2017) are largely not applicable to Vietnam. Proposed solutions like reducing birth rate, improving health, reducing poverty, developing sustainable land-use initiatives, and livestock breeding may be effective in the long run, but for the various extremely rare and highly endangered primate species of Vietnam there is not enough time remaining to just rely on long-term developments.

2.2. Law enforcement

Estrada et al. (2017) do not explicitly mention law enforcement as a tool for improving conservation. However, in Vietnam this is one of the most critical points. One of the primary reasons for the immense volume of wildlife in the illegal trade and the dramatic decline of wild animal populations - not only primates – is the result of an ineffective, unmotivated, and apathetic enforcement of the existing laws. In turn, this result from rudimentary knowledge, training, and education of the forest protection authorities, especially the ranger force on the ground and their restricted authority to act, compared to police and other law enforcement authorities. Only about 10% of the rangers working in the field are trained and educated in biodiversity conservation (Viet Nam News, 2016c). The path for forest protection authorities to prosecute a considerable number of violations is complicated, and the justice department is often unable to cope with offenses in wildlife crime (Education for Nature – Vietnam, 2017).

Vietnam Forest Authorities stated: "illegal trafficking of wildlife or hunting of endangered animals in forests has concerned state agencies and biologists recently" (Viet Nam News, 2016), implying that state agencies and biologists just recently noticed the problems, which is not accurate. For decades, and at least since the enactment of the first law for protecting animals in 1992 (Decree 18/HdBT), hundreds of reports on wildlife, wildlife trade, programs and regulations recommended urgent and stronger law enforcement, with minimal impact to the actual practise of protection.

2.3. Expansion of protected areas

With 2.27 million ha of protected area, or 6.8% of the countries land territory, Vietnam provides relatively good conditions for the protection of natural resources including fauna and flora. However, a high number of the protected areas are small and/or fragmented, and are therefore more vulnerable to impacts while also allowing for easier access. In many cases, adjacent unprotected areas possess the same habitat, but they are reserved for other use and often without any detailed prospective planning. Under the extreme threat to many endangered species and habitats, the extension of existing protected areas to provide a larger and safer habitat should be considered. The procedure for the extension of an existing protected area is intricate and lengthy. The clarification of landownership and support of local authorities can be cumbersome even if no private land is included.

One example is the extension of Van Long Nature Reserve which holds the only viable population of the 'Critically Endangered' Delacour's langur, one of the world's rarest primate. The population in the nature reserve is well protected and growing, but to secure the long-term survival and genetic diversity it would be necessary to increase the size of the protected area to about 7,000 ha by including an adjacent area with intact habitat. A considerable obstacle of the extension is the fact that this areas belongs to the neighbouring provinces.

A focus in conservation through allocation of land and suitable habitat should be the concentration of funds and protection activities on a lower number of larger areas, instead of a high number of small and scattered areas.

2.4. Captive breeding and reintroduction

The long-term survival of a species depends on the survival of a viable population in an intact habitat in the wild. The future for many of Vietnam's primate species is not safeguarded, and particularly for those species on the precipice of extinction including the Delacour's langur, Cat Ba langur (*T. poliocephalus*), Francois' langur (*T. francoisi*), Hatinh langur (*T. hatinhensis*), Tonkin snub-nosed monkey (*Rhinopithecus avunculus*), eastern and western black gibbons (*Nomascus nasutus* and *N. concolor*) and northern and southern white-cheeked gibbons (*N. leucogenys* and *N. siki*).

Captive breeding and reintroduction are costly conservation interventions and should be considered only if preservation in the wild is currently impractical or unsuccessful. As part of this action, extensive and targeted capturing of wild individuals would be required. However, with the high level of illegal hunting in Vietnam, confiscated individuals can be a founder stock for captive breeding programs. This was successfully implemented by the EPRC with the Delacour's langurs, Cat Ba langur, the grey-shanked douc langur and the northern and southern white-cheeked gibbons.

The reintroduction of captive born Delacour's langurs was implemented as a pilot study (Elser, 2014; Elser et al., 2015). The success of this project greatly relied on the support and awareness of the communes surrounding the reintroduction site; Van Long Nature Reserve (Elser & Nguyen Hong Chung, 2013). A reintroduction program for Hatinh langurs is currently in progress. The goal is the establishment of a viable population in Ke Go Nature Reserve, Hatinh Province, which is an area where the species was eradicated. For one of the world's rarest primates, the Cat Ba langur, focus should be on enlarging the captive population and implementing a captive breeding program, rather than translocating.

The implementation of a captive breeding program for many primate species has already been in place for more than twenty years at the EPRC, which is less cost effective than reintroduction itself. A relatively high investment is required to eliminate or at least reduce poaching in the area chosen for reintroduction. It is also necessary to improve ranger work through training and to stimulate motivation, and it is extremely important to involve surrounding communes in the project, and receive their acceptance and support. This, however, is only possible in a long and intensively organized process.

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The ranging patterns of reintroduced pygmy slow lorises (*Nycticebus pygmaeus*) in Cuc Phuong National Park, Vietnam

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Key words: Home ranges, nocturnal primate, translocation, Southeast Asia, Lorisidae

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Summary

The pygmy slow loris (*Nycticebus pygmaeus*) is threatened by hunting and deforestation throughout its range countries. To restock wild populations several organizations use reintroduction as a conservation strategy. In the pygmy slow loris and other *Nycticebus* species reintroductions have yielded low survival rates, leading many to question the welfare of released individuals and the conservation value of reintroduction. In response to these concerns, researchers have begun to investigate critically various aspects of slow loris reintroduction. Here we evaluated the ranging patterns of six released pygmy slow lorises in the former botanical garden of Cuc Phuong National Park, Vietnam. Following ten months of staggered releases and nightly observations, we recorded the nightly movement of three male and three female adult pygmy slow lorises. The mean home range size in males was 81±105 ha (Minimum Convex Polygon); 25±31 ha (Kernel Contouring) and in females 0±2 ha (Minimum Convex Polygon); 9±5 ha (Kernel Contouring). Observed home range sizes in males were larger than those reported for wild and reintroduced pygmy slow lorises. Individuals dispersed out of the release site (N=1), lost their collar or signal (N=2), or were found dead (N=2). A number of factors including territoriality, natal habitat preference induction, and stress play a role in the observed results. Future reintroductions should select a release site with more space than seen in wild home ranges, as released individuals maintain larger home ranges while in a novel environment, as well as consider how individual experiences can have a lasting effect on fitness.

Mô hình di chuyển của loài Culi nhỏ (*Nycticebus pygmaeus*) được di dời đến Vườn Quốc gia Cúc Phương, Việt Nam

Tóm tắt

Loài Culi nhỏ bị đe dọa bởi nạn săn bắn và phá rừng tại tất cả những nước mà loài có sự phân bố. Nhằm tăng số cá thể trong quần thể, một vài tổ chức bảo tồn đã chọn giải pháp di dời các cá thể bị đe dọa và tái hòa nhập chúng như là một chiến lược bảo tồn. Đối với loài Culi nhỏ và những loài khác thuộc giống Nycticebus giải pháp này thường có tỷ lệ sống sót thấp. Do đó, nhiều câu hỏi về sự an toàn của các cá thể được di dời và giá trị bảo tồn của giải pháp này đã được đặt ra. Để tìm câu trả lời, nhóm nghiên cứu đã tiến hành điều tra những yếu tố quan trọng trong di dời loài Culi lớn. Trong nghiên cứu này, chúng tôi đánh giá mô hình di chuyển của 6 cá thể loài Culi nhỏ được di dời vào vườn thực vật cũ của Vườn quốc gia Cúc Phương, Việt Nam.

Chúng tôi đã theo dõi số cá thể nghiên cứu trong đêm và ghi chép sự di chuyển của 3 cá thể đực và 3 cá thể cái trưởng thành, loài Culi nhỏ. Kết quả cho thấy, vùng sống trung bình của các cá thể đực là 81± 105 ha (MCP); 25±31 ha (KC) và 10±2 ha (MCP); 9±5 ha (KC) đối với các cá thể cái. So sánh kết quả về vùng sống trung bình ở nhóm đối tượng nghiên cứu cho thấy vùng sống trong nghiên cứu này cao hơn trong tự nhiên ở cùng loài và cao hơn vùng sống của loài Culi lớn được di dời. Số cá thể di chuyển ra khỏi khu vực nghiên cứu là 1 cá thể (N=1), mất vòng đeo cổ là 2 cá thể (N=2) và chết là 2 cá thể (N=2). Một số yếu tố ảnh hưởng được xem xét là tập tính bảo vệ vùng sống, sự thay đổi môi trường sống ưu thích, và stress. Chúng tôi đề xuất cho những lần di dời sau nên tìm những vị trí có không gian rộng hơn, bởi vì những cá thể được di dời cần vùng sống rộng hơn. Đồng thời cần xem xét kinh nghiệm của từng cá thể trong việc thích nghi với môi trường mới.

Introduction

The pygmy slow loris (*Nycticebus pygmaeus*) (hereafter the pygmy loris) is one of 21 primate species in Vietnam listed as 'Critically Endangered', 'Endangered', 'Vulnerable', or 'Near Threatened' (Roos et al., 2013), largely due to hunting for the pet trade, use in traditional medicine and deforestation (Fooden, 1996; Ratajszczak, 1998; Groves, 2007; Nadler & Brockman, 2014; Nekaris & Starr, 2015). The pygmy loris, like other *Nycticebus* species, is characterised by an unusually long life history relative to body size, slow climbing locomotion, exudativourous diet, nocturnality, and use of torpor (Duckworth, 1994; Nekaris & Bearder, 2011; Rasmussen & Izard, 1988; Ruf et al., 2015; Streicher, 2009). Following years of popularity as a 'social media star' linked with unsustainable wildlife trade, the pygmy loris was up-listed on the International Union for Conservation of Nature (IUCN) Red List from 'Vulnerable' to 'Endangered' in 2016 (pers. comm. Nekaris). As a result of the above-mentioned characteristics and their poor affinity for captivity, the continuous hunting pressure placed on this species is particularly destructive.

Translocation, defined by the IUCN as "the deliberate and mediated movement of wild individuals from one part of their range to another" (IUCN, 2013), is an important conservation tool used to combat high numbers of declining animal populations. Translocation is the overarching term used to define any form of population restoration – reinforcement or reintroduction - and conservation introduction. Despite its frequent use and purported importance to conservation, historically reintroductions have a low success rate (Griffith et al., 1989); the causes of these failures are poorly understood due to the difficulty of post-release monitoring (Fisher & Lindenmayer, 2000) and reluctance to publish negative outcomes. Furthermore, difficulties arise with the way we define success; is it the creation of a self-sustaining population or a pre-determined period of survival immediately following the release? The success or failure of reintroduction is dependent upon short- and long-term processes, including the immediate reaction of releasees to the novel area and the social dynamics of creating a new functional population (Armstrong et al., 1999). Intensive post-release monitoring allows us to determine whether a population that disappears following release has succumbed to stochastic demographic processes, increased post-release mortality, or post-release dispersal (Armstrong et al., 1999). Data on these various components of post-release are important, as they allow the identification of the mechanisms responsible for success or failure of translocation efforts (Griffith et al., 1989; Armstrong et al., 1999).

Only a handful of organisations use systematic slow loris reintroduction and post-release monitoring as a practical, yet expensive strategy to aid in replenishing wild populations, with an attempt at adherence to IUCN Reintroduction Specialist group policies. Throughout their range translocations of *Nycticebus* spp. occur that violate IUCN recommendations to the extent of introducing species outside of their endemic range. This practice may be due to government agencies requiring animals be returned to the wild immediately (Streicher, 2004), but it is also largely due to misconceptions regarding beneficial actions for individual welfare and conservation. Concerns regarding the welfare of translocated individuals have also risen with the increase in unsuccessful and unmonitored releases (Moore et al., 2014). To avoid arbitrary primate releases, it has become increasingly important for organizations to develop a conservation strategy that includes well-planned and well-monitored reintroductions to document and share their work, whether successful or unsuccessful (Kumar et al., 2015). Nekaris & Starr (2015) noted that the limited success of slow loris translocations was associated with scarce knowledge on social, behavioural, and ecological factors, including the variability across species, within this genus.

In Vietnam pygmy loris reintroductions have been systematically carried out with published results by two rescue centres, the Endangered Primate Rescue Center (EPRC) in Cuc Phuong National Park, about 130 km south of Hanoi, and the Endangered Asian Species Trust (EAST) in the Cat Tien National Park about 150 km north of Ho Chi Minh City. The EPRC was the first to report their reintroduction and post-release monitoring of pygmy lorises in 2000 releasing nine individuals into the Cuc Phuong

National Park (Streicher & Nadler, 2003; Streicher, 2004). Streicher & Nadler (2003) observed a high intake of insects and exudates in the released individuals and their sensitivity to cooler temperatures, noting hypothermia as a possible cause of death. EAST has reported on more than 20 released pygmy lorises since 2009 (Kenyon et al., 2014). Kenyon et al. (2014) noted that reintroduced pygmy lorises had a mean home range size of 20 ha, required at least two days in an *in-situ* release cage, and the ideal release season was between June and November (wet season). Following a wild study on this species in Cambodia, Starr (2011) noted that knowledge of the spacing and mating systems of the pygmy loris may lead to the development of useful *in-situ* and *ex-situ* conservation strategies, aiding in estimating population size and the carrying capacity of wild populations. She reported a mean home range size of 22 ha in males and 12 ha in females (Starr 2011).

Home range formation and ranging patterns are essential aspects of long-term survival in all animal species (Schick et al., 2008). Ecological, behavioural, and social factors are known to influence ranging patterns in primate species; researchers have even associated the size and formation of home ranges with stress, specifically in reintroduced individuals (Nekaris, 2011). When trying to establish or re-establish a population, dispersal from a release area is a concern, since this will decrease the number of possible founders and will expose individuals to unknown factors outside of the release site (Allen et al., 1993; Clarke & Schedvin, 1997). Natal habitat preference induction (NHPI) can cause post-release dispersal as some animals show a preference for areas that resemble their natal range (Davis & Stamp, 2004). During the establishment phase of translocations the mortality rates can be higher than seen in a normal population, due to stress and the inexperience of released individuals (Tweed et al., 2003).

In this paper we focus on the ranging patterns of six translocated pygmy lorises at Cuc Phuong National Park. Our aim is to examine their home range formation and to discuss possible contributing factors to the fitness and potential survival of the individual pygmy lorises.

Methods

Reintroduction

All pygmy lorises included in this reintroduction were residents at the EPRC having been confiscated in Vietnam. Once deemed appropriate for release, staggered pair releases took place between October 2014 and June 2015. Prior to release each pygmy loris spent two-three days in a medium sized in-situ pre-release cage (Fig. 1). Releases occurred between 6pm to 8pm, and released individuals were observed using a red-filter head torch (Clulite®).

Fig.1. The temporary release cage at the reintroduction site.

Release Site

The release site was the Cuc Phuong National Park Botanical Garden, the same site used in the EPRC's first release in 2004. Relying on informal accounts, no pygmy loris population has been seen since this initial release, but no formal population survey was conducted prior to the releases in this study. Strictly based on the same criteria used in 2004, which is the sighting of a wild pygmy loris in 1999, the site was deemed a suitable release site in this study (Streicher & Nadler, 2003). During retrospective surveys there was no presence of predators and the fence surrounding the 120 ha area provided added security from hunters. Characterised by tall continuous tree coverage, a dense variety of vegetation, and large limestone hills covered in sparse primary forest. As the area was a former plantation, many trees have remained in planted rows but much of the area has become overgrown, further contributing to the vines and branches that increased connectivity.

Radio-tracking

Each released pygmy loris was fitted with a collar (4 g Holohil® transmitters model PD-2C) prior to being placed in the pre-release cage at the release site (Fig. 2). This allowed us to track them on foot from the date of release until the lifespan of the collar elapsed, the collar fell off or trackers were unable to locate dispersing animals (Fig. 3). Staff members from the EPRC were trained in radio-tracking methods using an antenna and a handheld radio receiver (IcomInc® receiver model ICOM IC-R10) and each animal was located and observed each night between the hours of 6pm and 3am. When possible, prior to each night shift, sleeping sites were located, this aided in forming trails and locating individuals at night (Streicher & Nadler, 2003). Due to the dense vegetation in which pygmy lorises regularly slept, triangulation was used to pinpoint the location of an individual when it was not possible to make a reliable visual confirmation. GPS points were recorded on both a Garmin 64S and Garmin eTrex 10, by the observer (Fig. 4).

Fig.2. Pygmy loris fitted with a 4g radio collar (Holohil® transmitters model PD-2C). Photo Tilo Nadler.

Fig.3. Released pygmy loris with radio collar. Photo Tilo Nadler.

Fig.4. Daily night tracking to download the coordinates of the released lorises. Photo Tilo Nadler.

Home range calculation

Kenward (2001) defines home range as the area traversed during normal activity. Based on the techniques employed to analyse location data, the size and shape of a home range can appear differently (Lawson & Rogers, 1997). Minimum convex polygons (MCP) are commonly used and are easy to calculate. Kernel contouring (KC) uses more complex calculations to estimate the density of a distribution at any point (Seaman et al., 1998). Here we used both MCP and KC to analyse the GPS data in Ranges $8_{v2.16}$. (Anatrack LDT). We defined the home range as 95% of the area covered by the individual and the core area as 50% of the area covered (Pope et al., 2004; Sharpe & Goldingay, 2007). To calculate these areas, we analyzed the collected GPS points using a convex polygon with the selected cores of 95% and 50% and a focal site peel. Additionally, we analyzed data points using Kernel Contour with selected cores of 95% and 50%, a fixed kernel type, location density contours, and a smoothing multiplier of 1. We analyzed range overlap including areas within 95% and 50% of individual home ranges. To measure area development we performed an incremental area analysis with the same procedure used to calculate the home range sizes in both Minimum Convex Polygons and Kernel Contours in Ranges $8_{v2.16}$. (Kenward et al., 2008).

Statistical analyses

We used SPSS version 23 to calculate descriptive statistics, excluding outliers we calculated mean home range sizes and standard deviations, we also calculated median, which included all individuals. Home range sizes between males and females were compared using the non-parametric Mann-Whitney U test, with an alpha-value of 0.05 signifying significance.

Results

Home range size

The average home range size for males was 81±105 ha (MCP); 25±31 ha (KC), while the average size for females was 10±2 ha (MCP); 9±5 ha (KC). The median home range size for males was 156 ha (MCP); 47 ha (KC) and 9 ha (MCP); 2 ha (KC) for females. Though males maintained a larger home range compared to females there was no statistically significant difference. Table 1 details the individual home range areas, including the number of fixes. It is important to note that some lorises were observed for a longer period of time, which is evident in the number of fixes collected for each pygmy loris.

Table 1. Observed home range sizes of six pygmy lorises, presented in hectares (ha) for 50% and 95% of the home range calculated in Ranges $8_{v2.16}$ via Convex Polygons and Kernel Contouring. ± SD is provided where the mean home range size is presented between males and females.

ID	# of fixes	MCP 50% (ha)	MCP 95% (ha)	Kernel Contour 50% (ha)	Kernel Contour 95% (ha)
F_1	20	4.87	8.48	4.66	11.98
F_2	85	7.61	11.58	4.63	12.14
F_3	125	8.84	9.26	.58	2.49
Mean		**7.10±2.03**	**9.77±1.61**	**3.29±2.34**	**8.87±5.52**
Median		**7.61**	**9.26**	**4.63**	**11.98**
M_1	495	137.35	156.12	16.37	47.39
M_2*	65	601.72	669.65	48.51	196.71
M_3	145	.76	6.84	.54	3.21
Mean		**69.05±96.58**	**105.55±105.55**	**8.45±11.19**	**25.3±31.23**
Median		**137.35**	**156.12**	**16.37**	**47.39**

* Denotes excluded outlier

Overlap

All pygmy lorises overlapped within 95% of their home range (Fig. 5), at 50% of the home range, the core; there was less overlap (Fig. 6). Due to the staggered release and the variable number of days observed temporal overlap varies. M1 was present during the entire observation period and overlapped with all subsequent pygmy lorises. F3 and M3 overlap for one month in January 2015, while F1 and M2 overlapped in May and June 2015.

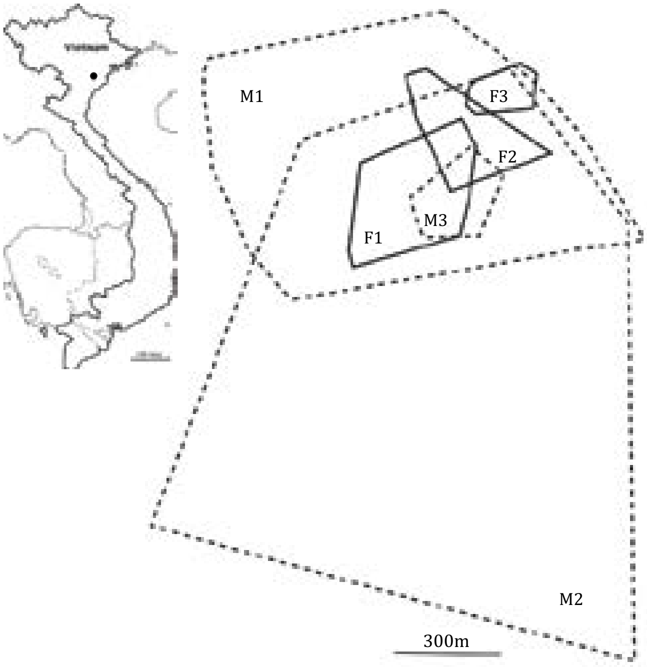


Fig.5. All pygmy lorises overlapped within 95% of their home range (Minimum Conex Polygons; males: dotted line, females: solid line). The study site is indicated by a black dot on the map of Vietnam.

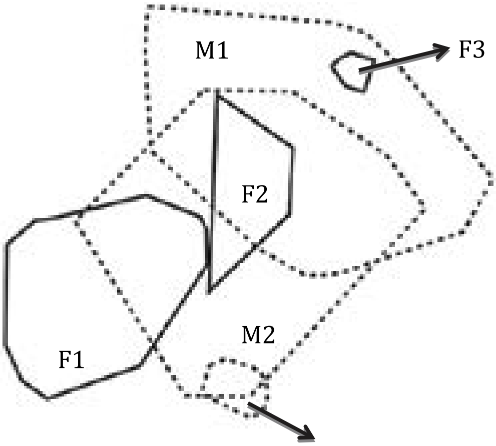
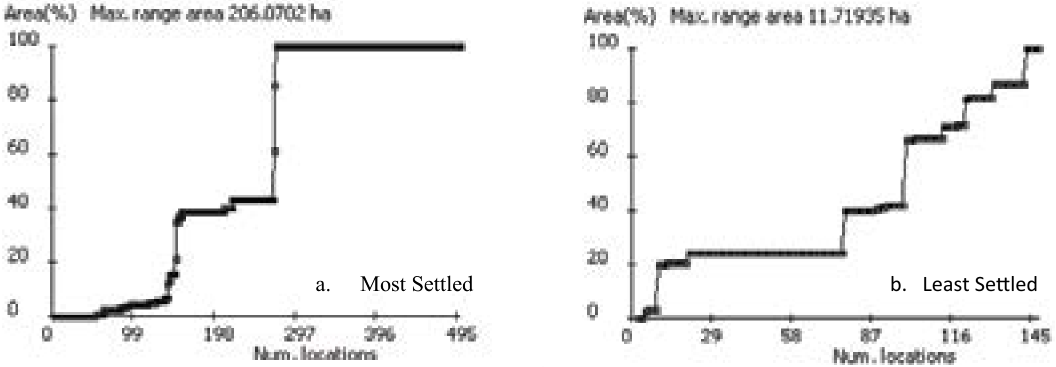


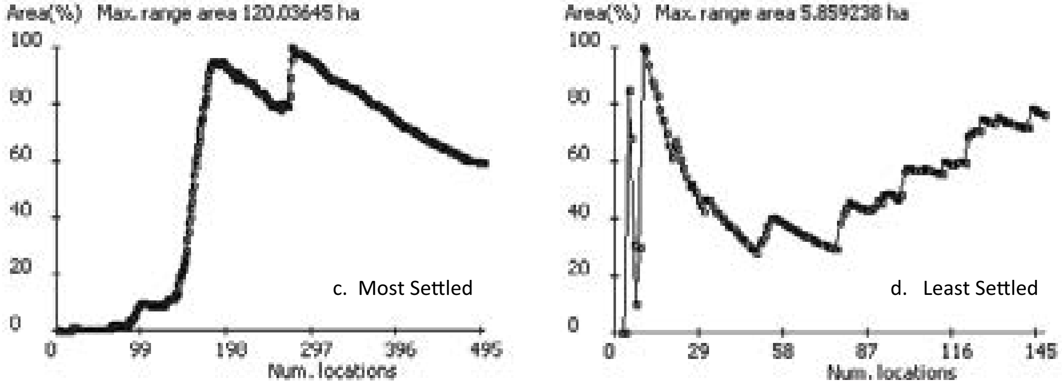
Fig.6. At 50% of the home range, the core; there was less overlap. (Minimum Conex Polygons; males:dotted line, females: solid line).

Incremental Area Development

The number of fixes it took before reaching a more stable home range was variable and some individuals never reached a consistent home range size during the study period. M1 was the only individual who displayed a graph where he plateaued at ~ 280 fixes (Fig. 7a). M3 continuously increased his area, never remaining consistent (Fig. 7b). The incremental areas differed between the method of analysis with MCP displaying more settlement and KC displaying a much less settled home range (Fig. 7c and 7d).



MCP



KC

Fig.7. Incremental area for M1 and M3, showing how individual settlement varies. The top two graphs were created using convex polygons and the bottom two were created using kernel contour. Max range area represents 100% of the home range.

Post-release Status

Of the six released pygmy lorises reported in this study, we only know that M1 settled into the release site. We suspect that F3 remained in the area as well, following occasional sightings of a habituated female with similar pelage throughout the observation period. Two pygmy lorises (F2 and M3) died of unknown causes, but there was no evidence of wounds indicating an attack. We lost F1's signal very early into the study period and she was never seen again. Following dispersal out of the release site we lost M2's signal, and we were unable to relocate him again.

Discussion

Homerange size and formation

Home range sizes in the reintroduced males were larger than those reported in wild pygmy lorises in Cambodia (Starr, 2011) and the translocated pygmy lorises in Dao Tien National Park (Kenyon et al., 2014). In this study individuals were lost due to long-range dispersal and detached collars. Of the published slow loris translocations, individuals traveling long distances and disappearing soon after release is a common problem (Streicher & Nadler, 2003; Streicher, 2004; Keyon et al., 2014). The incremental area development of these six released pygmy lorises provides a unique view on their ability to acclimate to a new area.

Measuring the development of pygmy loris home range can act as a proxy for adaptability in primates (Ossi & Kamilar, 2006), as it represents behavioural flexibility, showing how quickly an individual is able to settle into a new environment (Wright et al., 2010). In a study of wild and reintroduced Javan slow lorises (*Nycticebus javanicus*) in Indonesia, wild slow lorises displayed an incremental area development graph where 100% of their home range was identified in fewer fixes compared to the reintroduced slow lorises. Once they were observed in 100% of their home range the graphs plateaued showing that they were settled in the observed area, while the translocated Javan slow lorises continued to expand their area, which never stabilized (Nekaris & Rodes, 2013). In other translocated animals, unusually large or small home ranges, and previously unobserved ranging patterns are commonly reported, but many of these individuals normalize their behaviour in a matter of weeks or months (Molyneux et al., 2011; White et al., 2006; Tweed et al., 2003). The current observation period for this study included ten months, and a similar level of normalization was not observed, suggesting that these pygmy lorises were not as behaviourally flexible as the individuals or species in the above studies.

In regards to home range fidelity, Starr (2011) observed a saturation point after a range of 100 to 300 fixes between wild males and females. Here the first released male (M1) was the only pygmy loris that reached a point comparable to a saturation point seen in settled wild animals. To uncover the maximum area covered by M1 required 297 fixes. Other individuals' areas continued to grow suggesting instability in their home range formation. M2 maintained a small part of his ultimate area, but at the 40th fix, he moved to a completely new area, significantly widening his calculated home range.

Based on previous field reports of home range size, it was believed that the national park's former botanical garden (120 ha) would be large enough to support multiple pygmy lorises. The variation present not only between wild and translocated pygmy loris home ranges, but also between two translocated populations seems to be based on an unidentified factor, leading us to conclude that practitioners should overestimate the space needed for translocated pygmy lorises to establish a stable home range. During their release and in response to this novel environment, pygmy lorises will traverse large areas as they 'survey' the release site and hopefully settle into an ideal location within it. Kelt et al. (2014) observed larger home ranges in the reintroduced riparian brush rabbit (*Sylvilagus bachmani riparius*) compared to wild individuals, but hesitated to offer an explanation other than the effects of the varying topography. This may explain the differences seen between home range sizes reported at EAST and those observed at the EPRC.

Males tended to move outside of our discernible radio signal range, except for M1 who we were able to observe for the longest period of time. This individual was not only released first, but was released nearly two months before another male was reintroduced into an adjacent area. M2 and M3 spent the initial part of their post-release overlapping with M1, but eventually travelled far outside of his established territory. Partitioning territories is typical in wild slow and pygmy lorises as they are highly territorial (Fischer et al., 2003), but in this instance M1 maintained an unusually large home range of 156 ha (MCP)/47 ha (KC), accounting for all or half of the release site. The subsequent dispersal by M2 and M3 was no surprise, but the sheer size of M1's home range was surprising and caused M2 and M3 to move large distances to leave this claimed area. The home range reported for M2 is better described as a dispersal range, as he occupied very little of the area included in his calculated home range.

In contrast to the released males, the released females did not to our knowledge disperse out of the release site, and maintained smaller home ranges compared to those of the males. Reduced observation periods in females were largely due to lost and faulty collars; this also hindered our evaluation of their home range size. We did however continue to see these individuals within the release site throughout the observation period and on occasion we saw F2 and F3 interact with M1.

The overlap seen in the male and female home ranges further supports the proposed promiscuous mating system in pygmy lorises (Starr, 2011), which is contrary to the mating system seen in other *Nycticebus* species (Nekaris, 2014). Wiens & Zitzmann (2003) observed spatial groupings in greater slow loris (*N. coucang*) representative of a monogamous mating system and across slow loris species this is the accepted mating system. Female lorises are known to display aggression and territoriality, as they only share their wild territory with their offspring and one-three males (Nekaris et al., 2013). On the other end of the spectrum female tolerance has also been observed in captive Bengal slow loris (*N. bengalansis*) housed together in groups of three to four adults, their offspring and one male (Poindexter & Nekaris, 2014). Here we saw evidence of both the territorial and the tolerant female pygmy loris as they overlapped with each other in areas included in their 95% home range, but no overlap was observed in areas included in their 50% core area.

Stress

An animal's survival in a new environment depends on the individual's ability to: secure resources, orientate themselves, decide how to respond to environmental stimuli and maintain the location of conspecifics and predators (Teixeira et al., 2007). Mendl (1999) found that stress might influence animal survival by disrupting processes involved in decision-making. Hormones, such as epinephrine and vasopressin are released during stressful events, and can affect memory storage (Gold & van Buskirk, 1978). In a chronically stressed animal, the short-term behavioural changes needed to alleviate acute stressors no longer aid survival, but become harmful to the animal, leading to pathological conditions (McEwen, 1998). Transfer of an animal from a known area to a novel environment stimulates both the glucocorticoid response, which is associated with learning and memory, and the fight-or-flight response (Roozendaal et al., 1997; Hennessy et al., 1995). Stress can contribute to reintroduction failure by increasing the animal's vulnerability to the effects of chronic stress (Dicken et al., 2010). The direct cause for failure is likely external factors, but vulnerability to these external factors is worsened by chronic stress among the reintroduced individual.

Though we are unable to identify the exact cause of death in the deceased pygmy lorises in this study, there was no evidence of an attack from either a conspecific or a predator, leaving us to suspect that the cause was starvation, an illness, or poor acclimation to the environment. Starvation is often cited as a cause of mortality during the establishment phase of reintroductions (Islam et al., 2008; Rosatte et al., 2002; Work et al., 1999). The hypothalamic–pituitary–adrenal (HPA) axis plays a very important role in the regulation of food intake and metabolism (Dallman et al., 1993). A dysfunctional HPA axis, caused by chronic stress, will lead to both decreased feeding (Herzog et al., 2009) and increased energy requirements (García-Díaz et al., 2007) putting animals into a negative energy balance. Regardless of the suitability of the release site, this negative relationship will put the stressed reintroduced individual in a vulnerable position and much more susceptible to starvation, or other external factors. Additionally the pygmy lorises in this study travelled great distances throughout the observation period, causing them to exert extra energy.

Natal habitat preference induction (NHPI)

The post release dispersal seen in these pygmy lorises may be the result of NHPI. Even in cases where there is no question about the suitability of the release site, NHPI can lead released individuals to leave the release site seeking familiar environmental cues. Marbry & Stamps (2008) showed that brush mice (*Peromyscus boylii*) will settle in a habitat type similar to their natal habitat more than expected by chance. Hanghland & Larsen (2004) reported similar behaviour in red squirrels (*Tamiasciurus hudsonicus*) where given the choice between logged or intact conifers forest individuals selected the option that reflected their natal habitat. One major component of NHPI is associative learning; this speaks to the complex cognitive processes present in these species. Further study of the pygmy and slow loris cognitive capacity may shed light on the extent to which NHPI influences *Nycticebus* translocation successes. Unlike wild studies looking at NHPI the pygmy lorises in this study did not have the option to decide between habitat types. Our limited knowledge of their individual origin, especially their natal habitat type, limited the opportunity to include their characteristics as a criterion for release site selection.

Conclusion

Territoriality, chronic stress and the negative effects that stress can have on physiological process, as well as, NHPI are all possible explanations for the unusual ranging patterns and deaths seen in this reintroduction study. Following further examination and consideration, we conclude that the Cuc Phuong National Parks former botanical garden is no longer suitable for future pygmy loris releases. It is increasingly apparent that this area is not large enough to support multiple reintroduced male pygmy lorises. Having seen the post-release dispersal in the 2014-2015 release and the lack of a viable re-established population after the 2004 release, it is clear that some needed resources in this area are missing, or that the reintroduced individuals were not prepared to handle the added stressors associated with reintroductions. Beyond the former botanical gardens, Cuc Phuong National Park may have a flourishing population of pygmy lorises. Following population, predator, and forest structure surveys; it is possible to find a more suitable release site for future reintroductions. Though it was not particularly successful in this study, evident in the successes seen in Cat Tien National Park, reintroductions should still be considered a valuable conservation strategy for the pygmy loris. Learning from both successful and unsuccessful reintroduction programs is vital to improving practices for individual release candidates and for the species as a whole.

Acknowledgments

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Hibernation in pygmy lorises (*Nycticebus pygmaeus*) – what does it mean?

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Key words: South-East Asia, primate, torpor, multiday torpor, pygmy loris, hibernation

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Summary

Torpor use in primates appeared to be restricted to African species and was only recently discovered in a species from Asia, the pygmy loris (*Nycticebus pygmaeus*). This finding has considerable implications for our perception of torpor in this mammal group and demonstrates that torpor is probably more widespread in mammals than commonly thought. This article summarizes the current knowledge on the use of torpor in the pygmy loris and places it into the context of ongoing research on this topic.

Hiện tượng ngủ đông ở loài culi nhỏ (*Nycticebus pygmaeus*) – Ý nghĩa là gì?

Tóm tắt

Hiện tượng ngủ đông ở các loài linh trưởng được cho rằng chỉ tồn tại ở một số loài linh trưởng ở Châu Phi. Gần đây hiện tượng này được khám phá ở một loài linh trưởng ở Châu Á, loài culi nhỏ (*Nycticebus pygmaeus*). Phát hiện mới này có thể thay đổi nhận thức của chúng ta về hiện tượng ngủ đông ở nhóm thú này và nó cũng minh chứng rằng hiện tượng ngủ đông có thể phổ biến ở nhiều loài thú khác hơn những gì chúng ta thường nghĩ. Bài báo này tóm tắt những kiến thức hiện tại về việc sử dụng phương pháp ngủ đông ở loài culi nhỏ và đặt ra những vấn đề cần tiếp tục nghiên cứu đối với hiện tượng này.

Introduction

Animals in highly seasonal habitats face severe seasonal fluctuations of climatic conditions and often of resource availability. Ambient temperatures can be substantially lower during the cold season than during the hot season, requiring higher energetic expenses for endogenous heat production to maintain a high body temperature. Whilst the conditions during the hot season often provide a surplus of food, animals have to deal with food scarcity or low-quality food resources during the cold season. To overcome these challenges, many small heterothermic mammals display states of energy conservation such as daily torpor that lasts less than 24 hours, or multiday torpor that lasts more than 24 hours, commonly called hibernation. Daily torpor and hibernation are both characterized by a reduced metabolic rate, decreased activity, and reduced body temperature (e.g. Bieber et al., 2014; Hoelzl et al, 2015; Ruf & Geiser, 2015).

Recently we have reported hibernation in the pygmy loris, which was the first description of hibernation in a primate outside of Madagascar (Ruf et al., 2015). The pygmy slow loris or pygmy loris (*Nycticebus pygmaeus*) is a small, solitary, nocturnal primate, distributed east of the Mekong in Vietnam, eastern Cambodia, Laos and the southernmost part of China.The species is listed as 'Vulnerable' on the IUCN Red list of Threatened Species, due to an estimated population decline of more than 30% over the last two decades caused by habitat loss and poaching (Streicher et al., 2008).

Evidence of torpor in the pygmy loris

Pygmy lorises are members of the same suborder as lemurs, and have a small body with a weight rarely exceeding 400 g, which accounts for a high rate of heat loss (Fig. 1). They live partly in habitats with distinct seasonal fluctuations in ambient temperatures and food availability. Both body size and the seasonality of their habitats have previously given cause to assume that lorises might use torpor, and anecdotal evidence suggested that pygmy lorises undergo bouts of torpor during the cold season (Ratajszczak, 1998; Streicher, 2004).

Fig.1. Pygmy loris (*Nycticebus pygmaeus*) at the Endangered Primate Rescue Center. Photo Ulrike Streicher.

Daily torpor can be employed fairly spontaneously and often without restriction to specific seasons (Geiser, 2013); in contrast hibernation requires preparation in the form of accumulation of substantial energy reserves, usually stored in the forms of adipose tissue (Carey et al., 2003; Geiser, 2013). Pygmy lorises showed pronounced seasonal body weight changes, weighing up to 50% more in winter than during the hot summer months (Streicher, 2005), and were regularly found rigid and unresponsive during the cold winter months (Streicher, 2004). Therefore, they were an obvious candidate for a study on thermoregulatory processes.

Five individuals, housed at the Endangered Primate Rescue Center in Cuc Phuong National Park of northern Vietnam (Fig. 2), were implanted with data loggers to record their core body temperature (Ruf et al., 2015). Torpor was defined as body temperature below 30ºC for at least one hour. For three individuals winter data was collected, and these three individuals all used torpor between late October and early April (Fig. 3) (Ruf et al., 2015). The recorded torpor bout durations varied substantially, from less than 12 hours to over 24 hours (Fig. 4). The longest torpor bout recorded was 62.6 hours. This might seem relatively short, but it is longer than the maximum bout duration in four other hibernating species (including one lemur, Table 1), and comparable to the median maximum torpor bout duration in mammals, which is only 4.8 days (Ruf & Geiser, 2015). The occurrence of multiday torpor bouts, the fact that minimum body temperatures closely resembled ambient temperatures, and the weight gain and accumulation of adipose tissue prior to the cold season all identify pygmy lorisesas seasonal hibernators (Ruf & Geiser, 2015).

Fig.2. Outdoor enclosures for lorises at the Endangered Primate Rescue Center. Photo Ulrike Streicher.

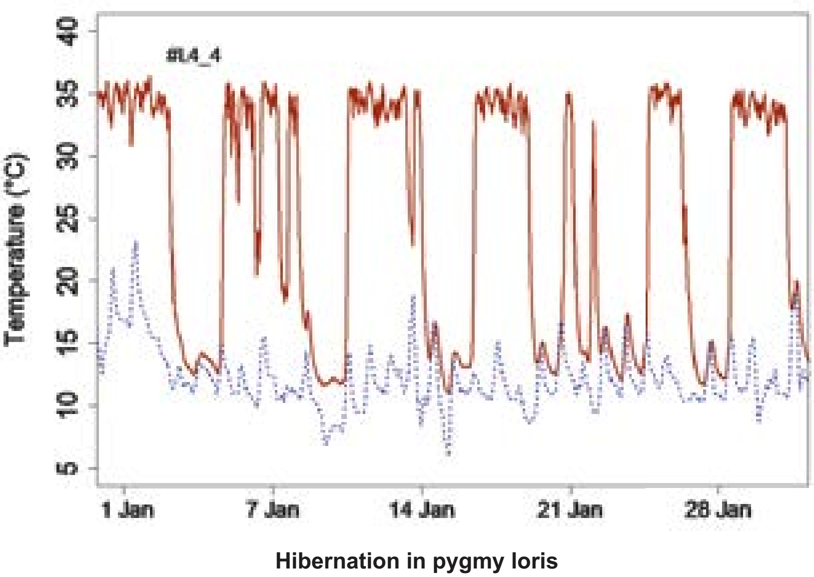

Fig.3. Core Tb (red line) in a pygmy slow lorises in midwinter, recorded over a four week period. The animal exhibited bouts of multiday torpor that is hibernation, interspersed with periods of euthermia and short torpor episodes. Blue line shows ambient air temperature.

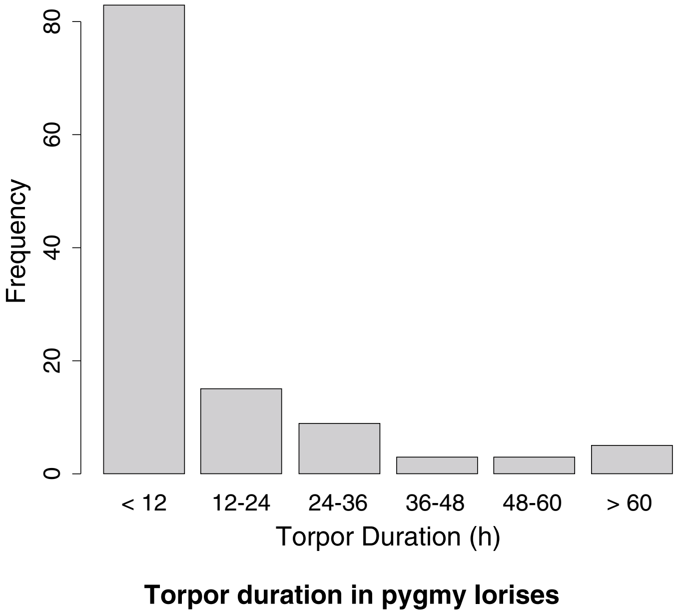

Fig.4. Animals (N = 3) exhibited both daily torpor (≤24h) or long phases of hibernation (or multi-day torpor) (≥24h).

Since study subjects were in captivity and not exposed to seasonal changes of food availability the occurrence of torpor was clearly not related to food availability. We assume torpor bout duration and frequency are even more pronounced in free-ranging individuals which experience seasonal food shortages. When provided with food *ad libitum* over winter, 'classical' hibernators such as the garden dormouse (*Eliomys quercinus*) exhibit short torpor bouts with a frequency distribution very similar to that of the pygmy loris shown in Fig. 3, with most torpor bouts lasting less than 24 hours (Daan, 1973). Torpor in the pygmy lorises was possibly triggered by ambient temperature and/or photo period, both well-known modulators of the timing of hibernationin the temperate zone (Körtner & Geiser, 2000; Malan, 1996). In contrast to many other hibernators, pygmy lorises do not retreat into burrows, but hibernate in relatively exposed locations (Streicher, 2004) and therefore are subjected exposed to highly varying ambient temperatures during torpor. The lorises predominantly entered torpor in the late night and early morning and remained torpid until the early afternoon (Ruf et al., 2015). They returned to euthermia when there was still sunlight available and well prior to the onset of their nocturnal activity, suggesting that they use sunbathing to reduce the energetic expenses required to return to euthermia after a torpor period, similar to many other tropical heterotherms (Schmid et al., 2000). Although torpor use allows for enormous energy savings, some species only use torpor opportunistically in response to acute energetic bottlenecks. There are costly trade-offs to energy savings during torpid periods such as slowed reactions (Nowack et al., 2016; Rojas et al., 2012), and reduced sensory abilities (Nowack et al., 2016) that potentially increase the risk of predation (but see Armitage, 2004; Bieber & Ruf, 2009; Turbill et al., 2011). Species using tree hollows or underground burrows are hidden and protected during torpor and often undergo hibernation for months (e.g. *Cheirogaleus sibreii*: Blanco et al. (2013); *Glis glis*: Hoelzl et al. (2015)), but pygmy lorises rest either in dense scrub or on exposed high terminal branches of trees (Streicher et al., 2003). An increased risk of predation might explain why torpor use was only observed on the coldest days during mid-winter (Ruf et al., 2015). In addition to expressing torpor and hibernation, pygmy lorises also slightly reduced their body temperature within euthermic levels on colder days, but not to levels below 30°C. Variability of body temperature likely allows lorises to remain alert and responsive to possible predators, while still permitting for energy savings (Glanville & Seebacher, 2010).

Table 1. Primate species for which heterothermy has been reported, including the maximum torpor bout duration (TBD) within the hibernation phase (in hours; not including uninterrupted hibernation when body temperature passively tracks ambient temperature. (T/H: T= daily heterotherm, H= hibernator, n.k.: not known).

Species	Common name	TBD (h)	T/H	Citation
LEMUROIDAE				
Cheirogaleus				
C. crossleyi	Furry-eared dwarf lemur	168	H	Blanco and Rahalinarivo (2010)
C. medius	Fat-tailed dwarf lemur	288	H	Dausmann et al. (2005)
C. major	Greater dwarf lemur	n.k.	H	Lahann (2007)
C. sibreei	Sibree's dwarf lemur		H	Blanco et al. (2013)
Microcebus				
M. berthae (published as M. myoxinus)	Madame Berthe's mouse lemur	19.2	T	Ortmann et al. (1997), Schmid et al. (2000)
M. griseorufus	Reddish-gray mouse lemur	61	H	Kobbe and Dausmann (2009), Kobbe et al. (2011)
M. lehilahytsara	Goodman's mouse lemur	n.k.	H	Blanco et al. (2016) Blanco et al. (2016)
M. imurinus	Grey mouse lemur	26 (captivity)	H	Schmid (2000),Schmid & Speakman (2000)
M. rufus	Brown mouse lemur	n.k.	H	Atsalis (1999), Randrianambinina et al. (2003)
M. ravelobensis	Gray brown mouse lemur	n.k.	T	Lovegrove et al. (2014)
Mirza				
M. coquereli	Coquerel's mouse lemur	n.k.	T	Dausmann (2008)
Allocebus				
A. trichotis	Hairy-eared dwarf lemur	n.k.	H	reviewed by Dausmann (2014)
LORISOIDAE GALAGIDAE				
Galagos				
G. moholi	African lesser bushbaby	10.1	T	Nowack et al. (2010), Nowack et al. (2013)
LORISIDAE				
Loris				
L. tardigradus tardigradus	Slender loris	n.k.	n.k.	Pers. obs. KAI Nekaris
Nycticebus				
N. javanicus	Javan slow loris	n.k.	n.k.	Pers. obs. KAI Nekaris
N. pygmaeus	Pygmy slow loris	62.6	H	Ruf et al. (2015)

Impact of the finding

Our study (Ruf et al, 2015) demonstrated that hibernation it is not restricted to primates of Madagascar. An earlier study already found daily torpor in a small primate from the African mainland, the lesser bushbaby (*Galago moholi*) (Nowack et al., 2013). However, in contrast to lorises, bushbabies only use torpor as an emergency strategy and may be unable to undergo prolonged phases of hibernation (Nowack et al., 2013). The hibernation found in an Asian primate and the daily torpor found in African bushbabies clearly indicate that these energy saving strategies are not a result of specific climatic conditions or evolutionary events unique to Madagascar, as was previously suggested (Dewar & Richard, 2007). On the contrary, torpor might have facilitated the colonization of Madagascar by lemurs and other terrestrial mammals (Kappeler, 2000; Martin, 1972; Nowack & Dausmann, 2015).

To date, torpor has been recorded in 12 lemur species of four genera of the same family in Madagascar (Table 1), one galago species in mainland Africa and one loris species in Vietnam. It is likely that further research will find hibernation and torpor in other primates living in seasonal habitats. There are also indications that the Javan slow loris (*Nycticebus javanicus*) and the slender loris, (*Loris tardigradus tardigradus*) might undergo states of decreased physiological activity such as torpor or even hibernation (Nekaris pers. com.). Tarsiers are another candidate for torpor (Lovegrove, 2012). Tarsiers are small (80–160 g), and exhibit the lowest euthermic body temperature (33.8°C) and basal metabolic rate (~65% of expected) of all primates (McNab, 1978). However, only a slight relaxation of euthermic body temperature regulation has been observed in this group with no evidence of pronounced torpor or hibernation (Lovegrove et al., 2014). Evidence of torpor in South American primates is entirely lacking (Alterman et al., 1995), but considering their small body sizes and variable climatic conditions further research might reveal torpor and hibernation among these primates as well.

Interestingly, torpor use in all primates seems to be restricted to the cold and dry season. It remains to be seen whether primates, as other hibernators (reviewed by Körtner & Geiser, 2000) have an endogeneous circannual clock that governs the timing of hibernation or if they entirely rely on external signals such as decreasing temperature and shortening photoperiod, and if primates are able to use torpor year-round in response to unexpected events.

Conclusion

We predict that, given the availability of increasingly smaller temperature recording devices with high storage capacity, torpor or hibernation will soon be detected in other primates. Many mammals and birds that are reluctant to exhibit torpor in captivity, even when kept in outdoor enclosures, readily undergo torpor in the wild (reviewed by Ruf & Geiser, 2015). Thus, it is likely that with an increasing number of studies on free-living animals the number of species known to use hibernation or daily torpor will further increase.

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Is all quadrupedalism the same? Form-function relationships in behaviorally distinct Asian colobines

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Summary

Gait mechanics in habitual quadrupedal primates has been explored thoroughly. However, little is known about the movements of quadrupedal primates that regularly engage in other, more specialized, forms of locomotion (e.g., suspensory or leaping). It is unclear whether the patterns of quadrupedal locomotion in these anatomically specialized species are compromised in some way compared to other more habitual quadrupeds. This study examined patterns of quadrupedal locomotion in two genera (*Pygathrix* and *Trachypithecus*) of Asian colobines. *Pygathrix* is well-known amongst the old-world monkeys for its unique ability to both walk quadrupedally above branches and to adopt arm-swinging locomotion similar to the gibbons. *Trachypithecus* are more typical arboreal quadrupeds which rarely exhibit suspensory locomotion. This study takes advantage of the highly diversified locomotor behavior observed within Asian colobines to determine if the use of arm-swinging *Pygathrix* effects the way species of this genus moves during quadrupedal locomotion compared to the movement of closely related non-suspensory colobines (*Trachypithecus*).

Results of a principal component analysis of locomotor variables demonstrate that quadrupedal locomotion of *Pygathrixis* different than that of *Trachypithecus*. These differences arise from variation in stride duration, elbow and knee flexion at touchdown and mid-stance, and hindlimb swing phase. The quadrupedal gaits of *Pygathrix* are characterized by some traits that increase security, but are also accompanied by a relatively more extended elbow and knee positions that act to increase the tendency for the animal to lose balance. Quadrupedal gaits of *Trachypithecus* are all similar to each other, representing minimal intrageneric variation.

Có phải tất cả các kiểu di chuyển bằng 4 chân đều giống nhau? Mối quan hệ giữa hình thái và chức năng của kiểu di chuyển này ở những loài colobine châu Á có sự khác biệt về tập tính

Tóm tắt

Hình dáng vận động kiểu di chuyển 4 chân thuần túy ở những loài thú linh trưởng đã được nghiên cứu nhiều. Tuy nhiên, kiến thức về những loài linh trưởng di chuyển 4 chân có sự kết hợp với những kiểu di chuyển khác như nhảy, tung người kiểu vượn vẫn còn ít được biết đến. Hiện tại vẫn chưa rõ kiểu di chuyển bằng 4 chân ở những loài đặc biệt này có sự liên quan nào với những loài còn lại. Nghiên cứu này phân tích mô hình di chuyển kiểu 4 chân ở hai giống đặc biệt *Pygathrix* và *Trachypithecus*. Giống *Pygathrix* được biết nhiều về khả năng đặc biệt trong các kiểu vận động khi vừa có thể đi bộ bằng 4 chân trên cành và di chuyển kiểu tung người giống vượn.

Giống *Trachypithecus* thì đặc trưng với kiểu di chuyển 4 chân trên cây và rất hiếm có kiểu vận động tung người. Nghiên cứu này đã có cơ hội ghi tập tính vận động đa dạng ở các loài colobine châu Á nhằm xác định tập tính vận động kiểu tung người ở giống *Pygathrix* ảnh hưởng ra sao đến kiểu vận bằng 4 chân, và so sánh với kiểu vận động bằng 4 chân của các loài thuộc giống *Trachypithecus*

Kết quả phân tích, so sánh về sự đa dạng trong các kiểu vận động đã chỉ ra rằng kiểu chi chuyển 4 chân ở giống *Pygathrix* thì khác biệt với giống *Trachypithecus.* Những khác biệt này được lý giải bởi: sự sai khác của sải chân, sự mềm dẻo của khuỷu tay và đầu gối khi đặt các chi xuống giá thể và thế đứng. Dáng đứng 4 chân ở *Pygathrix* nhằm tăng thêm sự vững chắc, và cũng đi kèm với xu hướng tăng sự cân bằng tạo bởi vị trí của đầu gối và khuỷu tay. Dáng đứng 4 chân của các loài thuộc *Trachypithecus* thì giống nhau và có ít sự khác biệt.

Introduction

In many taxa, morphology and behavior match the mechanical requirements of locomotion to produce an effective system. Gibbons have incredibly long arms compared to other primates, which serve to increase pendulum length thereby increasing the energetic efficiency of the system (Fleagle 1974; Granatosky 2016; Michilsens et al. 2011). Similarly, the bodies of hyenas are well-suited to long-distance travel over land. Along with this, they use walking and running gaits that minimize the metabolic cost of locomotion for their body plans (Spoor & Belterman 1986). In both of these cases, evolution has resulted in morphology and behavior that function efficiently in a single mode of locomotion. This is, however, not always the case. Consider the vampire bat that spends much of its time in flight, but must also maneuver on land (Riskin et al. 2006; Riskin & Hermanson 2005). As the result of having a body well-suited to flight, vampire bats are less agile on the ground than typical terrestrial mammals, and thus move quite differently as well (Riskin et al. 2005; Riskin & Hermanson 2005). In instances where an animal's morphology meets the requirements of more than one form of movement, studies of form and function become more complex. In these cases, compromises of a form in favor of another must be considered. Organisms that perform more than one type of locomotion offer insight into how animals might transition between modes of transportation over the course of their evolution.

Primates exhibit a remarkable diversity in locomotor capabilities, including a wide range of quadrupedal gaits both on arboreal and terrestrial supports, horizontal leaping and bounding, leaping between vertical supports, and arm-swinging (Fleagle 2013; Hunt et al. 1996; Napier and Napier 1967; Napier 1967). Quadrupedalism, however, remains the most common form of locomotion among primates and is often considered the basal form of locomotion for the order (Hunt et al. 1996; Rose 1973). All members of the order, with the exception of gibbons (Vereecke et al. 2006), are capable of moving quadrupedally for some distance (Fleagle 2013; Granatosky et al. 2016a; Napier and Napier 1967). The mechanical characteristics of quadrupedal walking are well-characterized for those primates that are considered habitual quadrupeds (Demes et al. 1994; Franz et al. 2005; Hildebrand 1967; Kimura et al. 1979; Larson et al. 2000; Schmitt 1999; Vilensky & Larson 1989). However, little is known about the movements of quadrupedal primates that regularly engage in other, more specialized, forms of locomotion [e.g., suspensory or leaping (Granatosky et al. 2016a) locomotion]. Furthermore, it is unclear whether the patterns of quadrupedal locomotion in these anatomically specialized species are compromised in some way compared to other more habitual quadrupeds.

Granatosky et al. (2016a) explored this issue by comparing the gait mechanics of arboreal quadrupedal locomotion in *Propithecus coquereli*, a dedicated vertical-clinging and leaping (VCL) primate to other species of quadrupedal lemurs. Vertical-clinging and leaping is a type of arboreal locomotion in which primates adopt orthograde postures at rest on vertically-orientated substrates. Movement is initiated through powerful hindlimb extension resulting in animals leaping from one vertical substrate to another (Crompton et al. 1993; Crompton et al. 2010; Demes et al. 1991; Fleagle 2013; Napier & Walker 1967; Stern and Oxnard 1973). The anatomy of VCL primates is characterized by relatively long hindlimbs compared to the short forelimbs (Burr et al. 1982; Connour et al. 2000; Demes et al. 1996; Gebo & Dagosto1988; Hall-Craggs 1965; Oxnard et al. 1981a;. 1981b; Ravosa et al. 1993; Schaefer & Nash 2007). This anatomical pattern is thought to make quadrupedal locomotion ungainly and inefficient (Wunderlich et al. 2014; 2011), but despite this, arboreal quadrupedal locomotion has been witnessed in a number of VCL primates, albeit rarely. Granatosky et al. (2016a) observed that during arboreal quadrupedal locomotion *P. coquereli* displayed locomotor patterns that were very similar to what was observed in other arboreal lemurs. The finding that *P. coquereli* adopts the characteristic patterns of primate arboreal locomotion provides evidence for the idea that these patterns may represent a basal primate gait condition, and that little variation in the mechanics of primate quadrupedal locomotion may be present.

In the present study, we test the effects of compromised behavior and morphology on the mechanics of quadrupedal locomotion using a multivariate approach. Specifically, we take advantage of the highly diversified locomotor behavior observed within the Asian colobines (Genus: *Pygathrix* and *Trachypithecus*) to determine if the use of arm-swinging, observed in *Pygathrix* (Byron & Covert 2004; Granatosky 2015; Su and Jablonski 2009; Workman & Covert 2005), effects the way species of this genus moves during quadrupedal locomotion compared to the movement of closely related non-suspensory colobines (i.e., *Trachypithecus*)(Wang et al. 2012).

The ability of the members of the genus *Pygathrix* to engage in arm-swinging locomotion has been well-documented (Byron & Covert 2004; Su & Jablonski 2009; Workman and Covert 2005). The kinetics and kinematics of arm-swinging in *Pygathrix* closely match data that has been reported in other species of arm-swinging primate [i.e., *Hylobates* and *Ateles*; (Granatosky 2015; Schmitt et al. 2016). Arm-swinging primates are faced with an unusual set of challenges compared to non-suspensory species (Andrews & Groves 1976; Fleagle 2013; Granatosky 2015; Granatosky 2016). Generally, large body-size makes upright quadrupedal locomotion difficult for suspensory species, as they are faced with an increased tendency to topple off the support (Cartmill 1985; Grand 1972). Consequently, slow and deliberate gaits may be necessary for these species when moving above branches (Cartmill 1985). Additionally, effective arm-swinging requires significant joint excursions and mobility in order to achieve pendulum-like locomotion, but this, in turn, results in relatively weak joints that cannot support high compressive loads (Granatosky 2016; Kimura et al. 1979; Larson 1998; Reynolds 1985). As a result, many highly suspensory primates demonstrate an unusual set of mechanisms to reduce weight-support on the forelimbs (Kimura et al. 1979; Larson 1998; Reynolds 1985). We hypothesize that *Pygathrix* will display specific gait mechanisms that are thought increase security and to reduce high compressive loads on the forelimb, and will, therefore, demonstrate aspects of their quadrupedal gaits that are distinct from the other Asian colobines. We also anticipate that members of the genus *Trachypithecus* will demonstrate few intrageneric gait differences, as quadrupedal locomotion remains the most commonly used form of movement within this genus.

Materials and Methods

Kinematic and spatiotemporal gait data were collected during arboreal quadrupedal locomotion from captive *P. nemaeus*, *P. cinerea*, *T. crespusculus*, *T. delacouri*, *T. hatinhensis*, and *T. poliocephalus* at the Endangered Primate Rescue Center in Cuc Phuong National Park, Nho Quan District, Ninh Binh Province following the protocols approved Duke's Institutional Animal Care and Use Committee. All animals were adults and were clear of any pathologies or gait abnormalities (Table 1). The methods used here have been described extensively elsewhere (Demes et al. 1994; Granatosky et al. 2016a; Granatosky 2016; Schmitt & Hanna 2004), and will only be summarized below.

The animals were videotaped from a lateral view during arboreal quadrupedal walking 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 (Granatosky et al. 2016b). All strides were collected while animals walked above a straight simulated arboreal simulated support (7.62 cm diameter). 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. As variation in speed has been shown to affect various aspects of locomotor performance, a non-parametric ANOVA was performed between the study species to determine if there were any significant differences in speed that may unintentionally confound the variables of interest.

From video recordings, we calculated diagonality, stride duration, stride distance, forelimb and hindlimb duty factor, and forelimb and hindlimb relative swing phase for each stride for each individual (see Table 2 for information about variables). Additionally, the position of the shoulder, hip, elbow, knee, wrist, and ankle 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, hip, elbow, and knee.All limb angles were digitized using DLT Dataviewer (Hedrick 2008) in MATLAB. All angular movements were measured in degrees (°). To make joint movements comparable between strides, different individuals, and different species, all joint data were scaled as a percentage of support phase. Shoulder and hip 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 and hip protraction, while angles less than 0° represent shoulder and hip retraction. Elbow and knee angles always reflect elbow and knee flexion, where 180° represents maximum elbow and knee extension. From the scaled data on joint movements, the general pattern of shoulder, hip, elbow, and ankle angular positions were compared statistically only at specific intervals [i.e., touchdown (when the limb comes in contact with the support), mid-stance (when the wrist comes to pass under the shoulder), and lift-off (when the limb leaves the support) for the knee and elbow, and touchdown and lift-off for the shoulder and hip].

Table 1. Animal subjects used in the study, primary locomotor mode repertoire for each species, and the number of strides analyzed for each species.

Species	Primary locomotor repertoire*	Number of individuals	Number strides analyzed
Pygathrix cinerea	Arboreal quadruped with some leaping, climbing. Suspensory behavior is common.	2	15
Pygathrix nemaeus	Arboreal quadruped with some leaping, climbing. Suspensory behavior is common.	4	7
Trachypithecus crepusculus	Arboreal quadruped with some climbing and leaping behavior. Suspensory behavior is rare.	2	11
Trachypithecus delacouri	Arboreal and terrestrial (karst landscape) quadruped with some climbing and leaping behavior. Suspensory behavior is rare.	2	6
Trachypithecus hatinhensis	Arboreal quadruped with some climbing and leaping behavior. Suspensory behavior is rare.	2	12
Trachypithecus poliocephalus	Arboreal and terrestrial (karst landscape) quadruped with some climbing and leaping behavior. Suspensory behavior is rare.	2	10

* Primary locomotor repertoire determined from Byron & Covert (2004), Su & Jablonski (2009), Workman & Covert 2005, and Workman & Schmitt (2012).

Table 2. Locomotor variables used to assess patterns of quadrupedal locomotion within the species analyzed in this study.*

Locomotor variable	Definition	Functional significance	Prediction for study species
Diagonality	The percentage of the stride cycle interval the footfall of a forelimb follows behind the ipsilateral hindlimb. Diagonality can be dividedinto five classes: (a) Lateral Sequence Lateral Couplets (0 ≤LSLC< 25); (b) Lateral Sequence Diagonal Couplets (25 ≤LSDC< 50); (c) Trot (= 50); (d) Diagonal Sequence Diagonal Couplets (50 < DSDC ≤ 75); and (e) Diagonal Sequence Lateral Couplets (75 < DSLC < 100).	Lateral-sequence, lateral-couplet footfall patterns are thought to prevent interlimb interference. However, this footfall pattern is thought to be inherently unstable because a majority (~66%) of the stride is spent as a unilateral bipod, which tends to roll the body side-to-side throughout the stride. Lateral-sequence, diagonal-couplet footfall patterns are more stable than LSLC gaits due to the generally low proportion of the stride spent as a unilateral bipod (~22%), and the relatively high proportion of the stride spent as a diagonal bipod (only two contralateral limbs in contact with the support) and large tripod (three widely splayed limbs in contact with the support). Diagonal-sequence, diagonal-couplet footfall patterns, and trots maximizes the proportion of the stride in which the limbs are arranged as a widely splayed diagonal bipod. Diagonal-sequence, lateral-couplet footfall patterns are rarely observed.	Primates, in general, demonstrate an almost exclusive use of DSDC gaits. There may be a higher presence of LSLC in *Pygathrix* due to the slightly elongated limbs due to suspensory locomotion.
Stride duration	Defined as the amount of time (in seconds) from one right hindfoot touchdown to the next right hindfoot touchdown	Longer stride durations may indicate slower more deliberate forms of travel.	*Pygathrix* may demonstrate slower strides as a means to increase security while walking quadrupedally. Suspensory locomotion may be used for faster gaits.
Stride distance	Defined as the distance traveled (meters) from one right hindfoot touchdown to the next right hindfoot touchdown	Longer stride distances may indicate more energetically efficient locomotion. Additionally, during arboreal locomotion increased stride distance results in a lower number of times the animal makes contact with the substrate for a given distance. Lower stride frequency results in lower substrate oscillations resulting in more secure arboreal locomotion.	*Pygathrix* may demonstrate longer stride distances due to the slightly elongated limbs due to suspensory locomotion.

Duty factor	The amount of time the limb (forelimb or hindlimb) is in contact with the support (sec) divided by the duration of the stride (sec)	Longer duty factors are associated with a greater relative time the limb is in contact with the support. Longer duty factors may represent a mechanism for increased security during locomotion.	*Pygathrix* may contact the support longer to increase security while walking on top of thin supports.
Relative swing phase	The amount of time the limb (forelimb or hindlimb) is not in contact with the support (sec) divided by the duration of the stride (sec)	Shorter relative swing phases are associated with a shorter relative time the limb is not in contact with the support. Shorter relative swing phases may represent a mechanism for increased security during locomotion.	*Pygathrix* may reduce swing phase as a means to increase security while walking on top of thin supports.
Shoulder and hip protraction and retraction	Limb protraction and retraction is the angle of the humerus and femur relative to the vertical axis of the limb at the beginning, middle, and end of stance phase (Schmitt 2011).	Depending on the stiffness of the limb, increased protraction can result in decreasedpeak vertical forces and increased vertical oscillations of the center of mass (COM), which can influence the energetic costs and security of movement. Greater protraction and retraction can also result in increased stride distance (see explanation above)	*Pygathrix* may demonstrate increased shoulder and hip protraction and retraction to reduce peak vertical forces on the forelimbs and reduce oscillations of the COM.
Elbow and knee flexion	Elbow flexion measured as the internal angle between the shoulder, elbow, and wrist. Knee flexion measured as the internal angle between the hip, knee, and ankle.	Largely as a measure of limb stiffness that may influence both load and possibly oscillations of the COM. Changes in limb yield have been implicated as part of the explanation for the unusual distribution of forces in primates in which peak forces are generally higher on the hindlimbs than they are on the forelimbs. Crouched limb postures may also be associated with increasing balance on thin arboreal supports.	*Pygathrix* may demonstrate increased elbow and limb flexion to reduce peak vertical forces on the forelimbs and increase balance on thin arboreal supports.

* Definitions, functions, and interpretations derived from Granatosky (2016),Karantanis et al. (2015), Larney & Larson (2004), Schmitt(1999 and 2011).

To compare locomotor behavior across groups we used principal components analysis (PCA) to create a three-dimensional representation of locomotion data. We chose this tool because PCA is the most effective way to represent multivariate data in the least variables possible (Sokal & Rohlf 2012). All data analyses were conducted using the custom-made software in MATLAB (MathWorks, 2016a). Measurements included in the PCA consisted of diagonality, stride duration, stride distance, forelimb and hindlimb duty factor, forelimb and hindlimb relative swing phase, and shoulder, hip elbow, and knee angle at touchdown, mid-stance, and lift-off. Shapiro-Wilk and Levene's tests were conducted to assure normality and equality of variances for the data. These statistical tests were conducted in JMP Pro ver. 12 (SAS; Cary, NC). Groups were then separated based on taxonomic affiliation, and distances between clouds of grouped data were analyzed using a mahalanobis distance calculation. The mahalanobis distance is calculated using standard deviation and mean of a cloud compared to a point; for all combinations of two groups, a "reference cloud" was chosen and a "test cloud" was chosen. We calculated the standard deviation and mean for the reference cloud. The mahalanobis distance is calculated as one unit per standard deviation from the center of the reference cloud. A mahalanobis distance was calculated for each point in the test cloud. The smallest five percent of distances were excluded and the next smallest point was recorded. Then, for that same combination of two groups, the test cloud is then used as a reference cloud and the reference cloud is used as a test cloud. If either of those two recorded points returns a value less than 1.96 standard deviations (the 0.95 benchmark) away from the center of the other cloud, those clouds are deemed insignificantly similar. If both of those returned values supersede the 1.96 distance benchmark, those clouds are deemed significantly different. Z values are represented by recorded mahalanobis distances and were used to calculate P values for further conviction regarding the significance of grouping differences. All P-values were adjusted for multiple comparisons by the Bonferroni method to account for type I error resulting from multiple comparisons. Although there has been considerable discussion recently concerning the possibility that adjustments for multiple comparisons like the Bonferroni method are too conservative (Nakagawa 2004), this study retains their use in order to make the most robust argument possible, while acknowledging that our significance may be a conservative estimate.

Results

Summary statistics for each species are reported in Table 3.The speed range between species was narrow, but significant differences were observed between *P. cinereaversusT. crepusculus* and *P. cinereaversusT. poliocephalus*. Results from the PCA analysis are shown in Table 4, as well as Figures 1, 2, and 3. The first three principal components account for 53.59% of all variance within the sample (Table 4). The first principal component accounts for 24.55% of all observed variation and separates *Pygathrix* from *Trachypithecus*. Factor scores on this axis are most highly correlated with stride time (positively), elbow position at mid-stance (positively), elbow position at touchdown (positively), knee position at mid-stance (positively), knee position at touchdown (positively), and hindlimb swing phase (negatively). Both species of *Pygathrix* had large positive mean values within this component. Conversely, all four *Trachypithecus* species were negatively valued on average; *T. crepusculus* and *T. delacouri* were close to zero, whereas *T. hatinhensis* and *T. poliocephalus* exhibited a much higher polarization from the *Pygathrix* groups along this axis. On average, *Pygathrix* groups demonstrate high scores on this axis and exhibit relatively longer stride times, more extended elbow and knee positions at touchdown and mid-stance, and relatively shorter swing phase in the hindlimb.

Table 3. Mean and standard deviation values for kinetic and spatiotemporal gait variables collected during quadrupedal locomotion in the study species.

Species	Pygathrix cinerea	Pygathrix nemaeus	Trachypithecus crepusculus	Trachypithecus delacouri	Trachypithecus hatinhensis	Trachypithecus poliocephalus
Speed (m/s)	0.62± 0.10	0.72 ± 0.18	0.97 ± 0.36	0.74 ± 0.18	0.83 ± 0.24	0.97 ± 0.28
Forelimb duty factor	0.61 ± 0.06	0.62 ± 0.07	0.63 ± 0.09	0.58 ± 0.08	0.57 ± 0.08	0.54 ± 0.05
Forelimb relative swing phase	0.39 ± 0.04	0.38 ± 0.06	0.45 ± 0.13	0.42 ± 0.12	0.37 ± 0.07	0.42 ± 0.04
Humeral angle TD (°)	116.61 ± 9.96	119.98 ± 9.99	115.44 ± 14.18	104.52 ± 11.46	109.23 ± 9.23	98.04 ± 7.23
Humeral angle LO (°)	35.55 ± 7.58	36.48 ± 6.64	29.17 ± 6.64	29.20 ± 4.08	29.62 ± 8.07	28.95 ± 4.83
Elbow flexion TD (°)	157.49 ± 7.12	164.55 ± 8.04	151.05 ± 13.43	144.26 ± 9.05	146.25 ± 8.66	142.54 ± 6.41

Elbow flexion MS (°)	135.83± 6.87	139.26± 9.09	124.89± 5.53	130.13± 9.46	127.23± 10.79	114.9± 6.78
Elbow flexion LO (°)	134.21 ± 8.96	140.03 ± 14.21	135.23 ± 11.73	136.97 ± 13.91	132.42 ± 11.07	127.09 ± 5.41
Hindlimb duty factor	0.65 ± 0.04	0.63 ± 0.03	0.64 ± 0.05	0.61 ± 0.03	0.61 ± 0.06	0.61 ± 0.04
Hindlimb relative swing phase	0.35 ± 0.04	0.37 ± 0.03	0.36 ± 0.05	0.39 ± 0.03	0.39 ± 0.06	0.39 ± 0.04
Hip angle TD (°)	132.92 ± 9.92	136.31 ± 9.37	139.24 ± 6.74	132.71 ± 6.41	136.12 ± 5.27	133.58 ± 3.94
Hipangle LO (°)	75.94 ± 12.17	73.50 ± 14.80	74.92 ± 11.72	76.14 ± 8.63	79.01 ± 11.64	78.68 ± 6.49
Kneeflexion TD (°)	154.68 ± 4.80	142.14 ± 10.70	145.14 ± 10.22	145.89 ± 5.12	141.16 ± 8.74	137.29 ± 3.64
Kneeflexion MS (°)	130.26 ± 6.48	123.80 ± 7.98	113.32 ± 6.85	122.94 ± 11.21	121.49 ± 5.67	113.51 ± 5.91
Kneeflexion LO (°)	136.36 ± 11.09	130.26 ± 17.89	123.33 ± 13.94	129.56 ± 10.66	118.73 ± 10.14	116.59 ± 7.24
Diagonality	0.63 ± 0.03	0.65 ± 0.06	0.61 ± 0.07	0.60 ± 0.04	0.61 ± 0.04	0.64 ± 0.06
Stride time (sec)	1.21 ± 0.09	1.13 ± 0.10	0.85 ± 0.11	0.98 ± 0.18	0.81 ± 0.14	0.80 ± 0.12
Stride distance (m)	0.74 ± 0.14	0.81 ± 0.15	0.79 ± 0.20	0.72 ± 0.19	0.71 ± 0.22	0.79 ± 0.10

$^{\text{TD}}$Touchdown, $^{\text{MS}}$Mid-stance, $^{\text{LO}}$Lift-off

Table 4. Principal component loadings for the first three axes of the principal component analysis performed on locomotor variables.

Variable	Factor 1	Number of individuals	Number strides analyzed
Forelimb duty factor	0.12	-0.20	0.43
Forelimb relative swing phase	-0.19	0.04	0.27
Humeral angle TD (°)	0.28	0.26	-0.18
Humeral angle LO (°)	0.27	-0.12	-0.15
Elbow flexion TD (°)	0.32	0.25	-0.10
Elbow flexion MS (°)	0.36	-0.01	0.07
Elbow flexion LO (°)	0.14	-0.13	-0.08
Hindlimb duty factor	0.26	-0.36	-0.24
Hindlimb relative swing phase	-0.26	0.35	0.24
Hip angle TD (°)	-0.06	0.06	-0.26
Hipangle LO (°)	-0.03	-0.47	-0.10
Kneeflexion TD (°)	0.27	0.12	0.31
Kneeflexion MS (°)	0.30	-0.05	0.31
Kneeflexion LO (°)	0.21	0.37	0.24
Diagonality	0.07	0.29	-0.34
Stride time (sec)	0.43	-0.01	0.00
Stride distance (m)	-0.03	0.29	-0.33

$^{\text{TD}}$Touchdown, $^{\text{MS}}$Mid-stance, $^{\text{LO}}$Lift-off

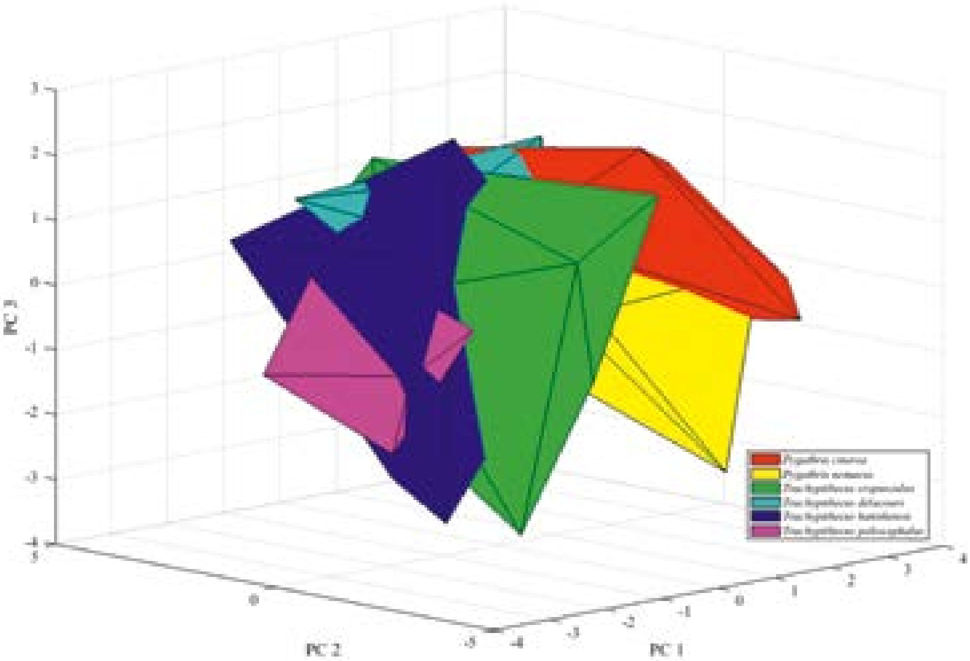

Fig.1. Three-dimensional convex hulls representing locomotor data during quadrupedal walking of six species of Asian colobine. Convex hulls encapsulate all data points for a particular species. Hulls were formed using factor scores for the first, second, and third principal component axes of variables describing locomotor behavior.

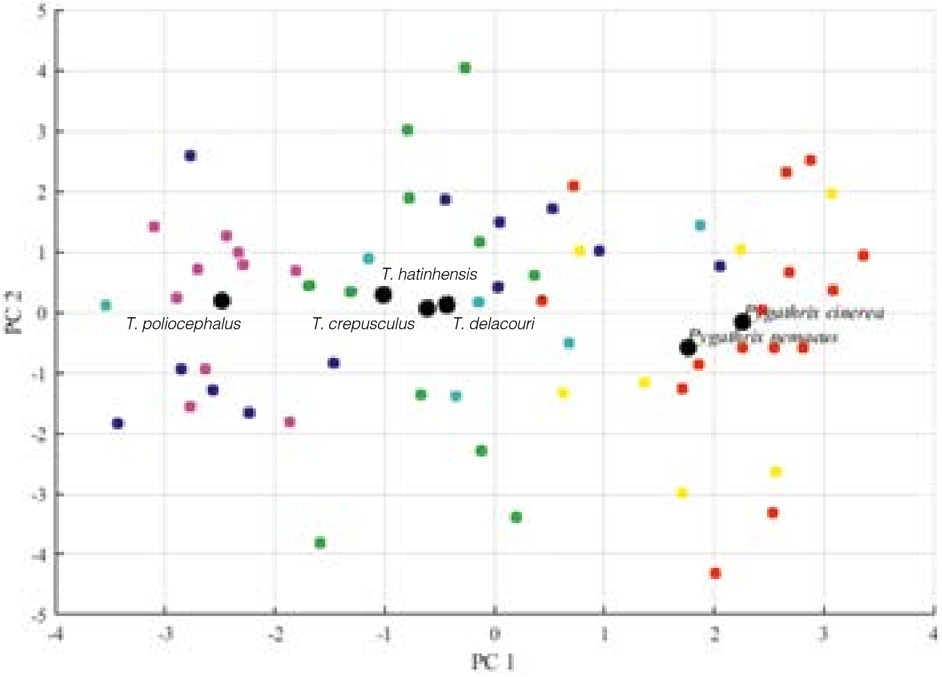

Fig.2. Principal component analysis of variables describing locomotor behavior during quadrupedal walking of six species of Asian colobine. Bivariate plot of factor scores for the first and second principal component axes of variables describing locomotor behavior. Data points presented as strides for each species [*Pygathrix cinerea* (red), *Pygathrix nemaeus* (yellow), *Trachypithecus crepusculus* (green), *Trachypithecus delacouri* (teal), *Trachypithecus hatinhensis* (blue), and *Trachypithecus poliocephalus* (pink)] with annotated points (black) representing each species means.

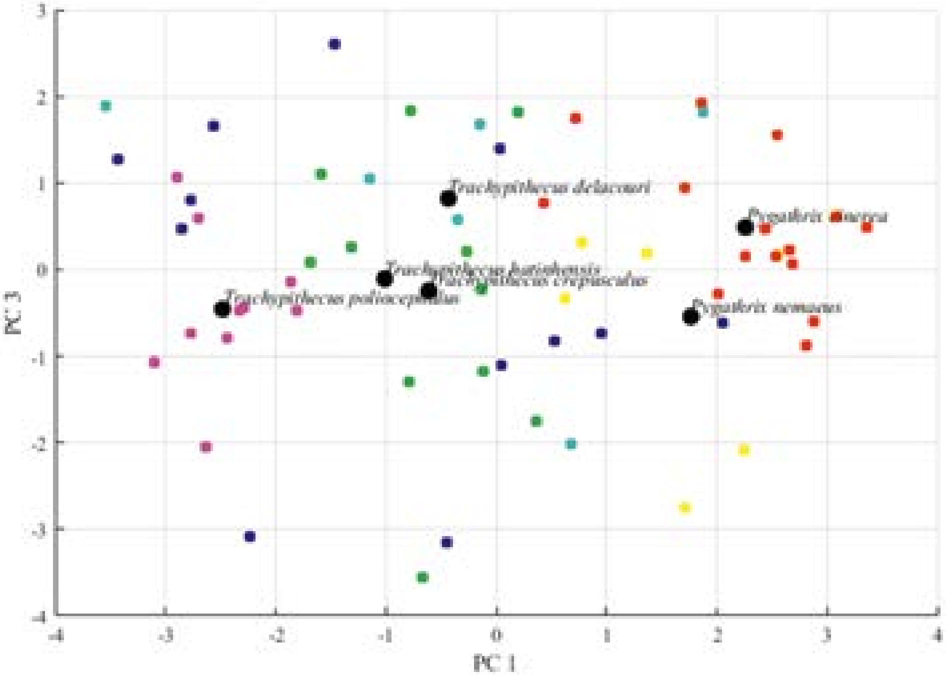

Fig.3. Principal component analysis of variables describing locomotor behavior during quadrupedal walking of six species of Asian colobine. Bivariate plot of factor scores for the first and third principal component axes of variables describing locomotor behavior. Data points presented as strides for each species [*Pygathrix cinerea* (red), *Pygathrix nemaeus* (yellow), *Trachypithecus crepusculus* (green), *Trachypithecus delacouri* (teal), *Trachypithecus hatinhensis* (blue), and *Trachypithecus poliocephalus* (pink)] with annotated points (black) representing each species means.

The second principal component axis accounts for 18.03% of all variance within the sample. Values for hip retraction (negatively), knee angle at lift-off (positively), hindlimb duty factor (negatively), stride distance (positively), and hindlimb swing phase (positively) largely determined position along the second principal component axis (Table 4). There was a greater deal of intraspecific variation along this axis than that of the first principal component. Mean values all remained near to zero, with *P. cinerea*, *T. delacouri*, *T. hatinhensis*, and *T. poliocephalus* presenting slightly positive means, and *P. nemaeus* and *T. crepusculus* presenting slightly negative means (Figures 1 and 2). Species with high scores on this axis exhibit relatively a lower level of hip retraction and extended knees at lift-off, relatively lower duty factor and longer hindlimb swing phase, and a relatively longer stride distance.

The third principal component accounts for 11.01% of the variation observed. The leading contributors to this variation include elbow angle at lift-off (negatively) and shoulder retraction (negatively). Like the second principal component, mean values of each species along the third principal component axis are close to zero. *Pygathrix cinerea*, *T. delacouri*, and *T. hatinhensis* occupy slightly positive positions on principal component three, while *P. nemaeus*, *T. crepusculus*, and *T. poliocephalus* occupy more negative positions (Figures 1 and 3). Animals with high values on this axis tend to have relatively flexed elbows and retracted hip positions at lift-off.

Based on our mahalanobis distance comparisons, *P. nemaeus* and *P. cinerea* were both found to be significantly different from all *Trachypithecus* species, but not from each other. Most intrageneric comparisons within *Trachypithecus* species were insignificant (Table 5). However, the locomotor patterns of *T. poliocephalus* were statistically different from both *T. crepusculus* and *T. delacouri*.

Table 5. Statistical comparison of all studied groups summarizing difference of locomotor behaviors. Bonferroni adjusted P-values used for statistical comparisons calculated using mahalanobis distances of scored variables. Bold text indicates significant differencebetween the locomotor behaviors of two species.

	Pygathrix nemaeus	*Trachypithecus crepusculus*	*Trachypithecus delacouri*	*Trachypithecus hatinhensis*	*Trachypithecus poliocephalus*
Pygathrix cinerea	0.075	**≤ 0.001**	**0.007**	**≤ 0.001**	**≤ 0.001**
Pygathrix nemaeus		**≤ 0.001**	**0.006**	**≤ 0.001**	**≤ 0.001**
Trachypithecus crepusculus			0.399	0.868	**≤ 0.001**
Trachypithecus delacouri				0.076	**≤ 0.001**
Trachypithecus hatinhensis					0.324

Discussion

Based on the results of our analysis, it is evident that quadrupedal walking gaits can be unique to individual species of primates, and, due to the close phylogenetic position of our study species (Wang et al. 2012), these differences are likely due to the functional demands of other locomotor compromises. In this study, we employed a novel means of analysis that has rarely been used to describe and compare locomotor data (Bergmann & Irschick 2010). The benefits of this technique are best explained through the number of criteria reviewed. In other methods of analysis, conclusions are drawn based on a small number of metrics. This method, conversely, allows us to represent a greater number of variables and thus we are able to paint a more comprehensive picture of locomotor patterns. Analyzing locomotor data using a PCA allows researchers an analytical means for assessing which traits selection likely acted upon by analyzing loadings. Therefore, use of this method may lead to new hypotheses and investigation about the evolution and functional consequences of those specific traits.

This study took advantage of the locomotor diversity observed in the Asian colobines (i.e., *Pygathrix* and *Trachypithecus*) to determine whether the presence of a large amount of suspensory locomotion within the locomotor repertoire of *Pygathrix* alters the patterns of quadrupedal locomotion of this species. This does appear to be the case, and most of the observed differences arise from variation in stride duration, elbow and knee flexion at touchdown and mid-stance, and hindlimb swing phase. In general, *Pygathrix* exhibit relatively longer stride times, more extended elbow and knee positions at touchdown and mid-stance, and relatively shorter swing phase in the hindlimb. The opposite pattern was observed in all four of species of *Trachypithecus*. These findings partially follow what was expected based on our knowledge and predictions of the locomotor traits we elected to analyze (see Table 2).

Pygathrix is a relatively large-bodied species (8-10 kg; Fleagle 2013) of arboreal primate. Large body size makes upright arboreal quadrupedal locomotion difficult as there is greater tendency for the animal to topple off the support (Cartmill 1985; Grand 1972). This tendency is accentuated by extended limb positions that raise the center of mass (COM) further away from the support. The quadrupedal gaits of *Pygathrix* are characterized by some traits that increase security (i.e., reduced swing phase and longer stride durations), but are also accompanied by a relatively more extended elbow and knee positions. This combination of features makes interpretation difficult. In addition to raising the COM higher above the support, thereby decreasing balance, extended limb positions in the forelimb do not dissipate forelimb peak vertical forces (Schmitt 1994, 1999). In other suspensory primates (e.g. *Ateles* and *Pongo*) mechanisms to reduce forelimb peak vertical forces are of the utmost importance due to the mobile, but weak, joints of the shoulder that are incapable of dealing with high compressive loads (Kimura et al. 1979; Reynolds 1985). It's possible that although suspensory locomotion does make up a significant proportion of *Pygathrix*'s locomotor repertoire, the fact that it is not as common as what is observed in other species (e.g. *Ateles*, *Hylobates*, and *Pongo*) may indicate that *Pygathrix* is not faced with the same mechanical stressors as these more obligate suspensory species. Further work comparing quadrupedal gaits of *Pygathrix* to those of some other suspensory primate (e.g. *Ateles*) should be conducted to address this possibility.

Among the four species of *Trachypithecus* analyzed, locomotor behavior was similar between all species as they occupied a similar region of locomotor morphospace distinct from *Pygathrix*. Although this result was anticipated, it is surprising that all four species should occupy such a similar locomotor morphospace, especially considering the use of "terrestrial" locomotion on limestone karst by *T. delacouri* and *T. poliocephalus* (Workman & Schmitt 2012). Although travel across rocks and cliffs by limestone langurs has been described as "terrestrial," limestone karst in Vietnam is an uneven, inclined, sharp, and dangerous substrate, unlike the ground traversed by conventionally terrestrial primates. Although limestone karst environments may be similar to terrestrial substrates in offering a greater opportunity for continuous pathways compared to a discontinuous arboreal canopy, there are notable differences in these rocky substrates. Limestone cliffs offer finite and often shear surfaces that represent a risk for falling that other terrestrial substrates do not. They must be gripped and balanced on. The mechanical requirements of moving and resting in this unusual habitat have been equated with the difficulty of arboreal movement (Workman & Schmitt 2012). Based on the results of our study it appears that evolution for movement on limestone landscapes has not drastically altered patterns of quadrupedal locomotion observed in other *Trachypithecus* species. This finding may be due to the controlled substrates used in our experimental design, and interesting future work could come from analyzing the locomotor behaviors of the different *Trachypithecus* species in their native habitats. Additionally, a further analysis comparing the locomotion of *Trachypithecus* to other arboreal and terrestrial old-world monkeys would help to elucidate this issue further.

It is important to note that there are limitations to this study, and these should be taken into account when interpreting the results of our analyses. As discussed above, variation in speed between species can result in substantial gait differences. Although we attempted to analyze only strides with similar speeds (i.e., only walking gaits were included), there was still significant variation in speed of these walking gaits between species (i.e. *P. cinerea* versus *T. crepusculus* and *P. cinerea* versus *T. poliocephalus*). Despite these observed speed difference, it appears that this did not substantially influence the results as *P. cinerea* also significantly differed from the other *Trachypithecus* species and not from *P. nemaeus*. Another potential problem is in our sample size of limited individuals and a limited number of strides collected for those individuals. With this in mind, the results reported in this study should be considered preliminary. It is important to note that the Asian colobines studied in this work are rare species in the wild and captivity. Limited individuals are available for research purposes, and all work done on these animals should be considered valuable due to a scarcity of samples.

Conclusions

This study provides one of the first analyses of locomotion in a multivariate context. The value of this type of analysis allows for focused investigation of meaningful locomotor variables that may be under greater selective pressure. Specifically, we take advantage of the highly diversified locomotor behavior observed within the Asian colobines (Genus: *Pygathrix* and *Trachypithecus*) to determine if the use of arm-swinging, observed in *Pygathrix*, effects the way species of this genus moves during quadrupedal locomotion compared to the movement of closely related non-suspensory colobines (i.e. *Trachypithecus*). Using our multivariate techniques we effectively demonstrated that the quadrupedal gaits of *Pygathrix* do indeed vary significantly from those of *Trachypithecus*. These differences arise from variation in stride duration, elbow and knee flexion at touchdown and mid-stance, and hindlimb swing phase.The quadrupedal gaits of *Pygathrix* are characterized by some traits that increase security but are also accompanied by relatively more extended elbow and knee positions that act to increase the tendency for the animal to lose balance. Quadrupedal gaits of *Trachypithecusare* all similar to each other, and low intrageneric variation.

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Inhibitory control in douc langurs (*Pygathrix nemaeus* and P. *cinerea*)

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Key words: inhibitory control, cognition, folivory, douc langurs, social complexity, dietary breadth

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Summary

Inhibitory control, defined as the ability to prevent pre-potent and unproductive actions, serves as a measure of cognitive skills in humans and non-human primates. Comparative research in this field revealed feeding ecology and aspects of social complexity, i.e. group size and fission-fusion dynamics, as reliable predictors for self-control in primates. Yet, these studies generally lack information on colobine species. Here we report the results of two self-control tasks conducted on folivorous and group-living red- and grey-shanked douc langurs. Altogether 17 captive animals were tested with a cylinder task and a middle-cup task. Both species revealed similar low levels of self-control, and, to the best of our knowledge, reached the lowest scores among all tested species in the cylinder task. Group size and fission-fusion dynamics cannot explain douc langurs' poor performances. Our results indicate that the intensity of social interactions within and between groups is more important for the development of inhibitory control than group composition. Douc langurs' poor self-control skills are in line with the performances of other folivorous primates promoting feeding ecology as good predictor for this cognitive skill.

Kiểm soát ức chế ở các loài Chà vá (*Pygathrix cinerea* và *P. nemaeus*)

Tóm tắt

Kiểm soát ức chế được định nghĩa là khả năng ngăn chặn các hành động bạo lực và không hữu ích. Khả năng này được xem như là một thước đo kỹ năng nhận thức ở người và thú linh trưởng. Những nghiên cứu so sánh trong lĩnh vực này cho thấy tập tính sinh thái dinh dưỡng cộng với sự phức tạp trong cấu trúc xã hội bao gồm: kích thước nhóm và tập tính tách nhập đàn là những chỉ thị đáng tin cậy để tìm hiểu khả năng tự kiểm soát ở các loài linh trưởng. Tuy nhiên, những nghiên cứu lĩnh vực này thường thiếu thông tin, dữ liệu trên các loài voọc. Dưới đây chúng tôi báo cáo kết quả thí nghiệm về khả năng tự kiểm soát được tiến hành trên loài khỉ ăn lá và sống theo đàn là voọc chà vá chân đỏ và chà vá chân xám. Tổng cộng 17 loài cá thể nuôi nhốt đã được thử nghiệm với một nhiệm vụ "xi lanh" và một nhiệm vụ với "cốc". Cả hai loài này cho kết quả ở mức độ thấp khả năng tự kiểm soát. Với sự hiểu biết của chúng tôi, cả hai loài đều đạt điểm số thấp nhất trong số tất cả các loài được thử nghiệm trong các nhiệm vụ tương tự. Quy mô nhóm và tập tính tách nhập đàn không thể giải thích màn trình diễn nghèo nàn của voọc chà vá. Kết quả cho thấy rằng cường độ các tương tác xã hội trong và giữa các bầy là quan trọng đối với sự phát triển của kiểm soát ức chế hơn so với thành phần cá thể trong bầy. Kỹ năng tự kiểm soát kém ở Voọc chà vá phù hợp với các loài linh trưởng chuyên ăn lá khác. Điều đó ủng hộ quan điểm sinh thái dinh dưỡng có thể dự báo tốt hơn về kỹ năng nhận thức này.

Introduction

Inhibitory control, also called self-control, is the capability of preventing pre-potent and unproductive behaviours (Hauser 1999) and serves as a measure of problem-solving skills in humans and nonhuman animals. In nonhuman animals, for instance, inhibitory control is required to prevent mating or feeding in the presence of higher-ranking conspecifics in order to avoid social conflict. Carnivores also require self-control when they pursue ambush predation strategies (MacNulty et al. 2007). Furthermore, inhibitory control is correlated with fitness in humans (Bezdjian et al. 2011; Mischel et al. 1989; Moffitt et al. 2011) and postulated to have positive influences on cognitive performances in primates (Amici et al. 2008; Schmitt & Fischer 2011; Wellman et al. 2011). Comparative analyses on self-control in 36 mammalian and bird species showed that self-control is widespread and this ability mostly strongly co-varies with absolute brain size (MacLean et al. 2014). In addition in primates, self-control was also positively correlated with dietary breadth but not with group size (MacLean et al. 2014). However, in another study conducted in several primates inhibitory skills were not related to variation in diet but to variation in social organization of the tested species, suggesting that social complexity is linked to inhibitory skills (Amici et al. 2008).

A species' feeding ecology has long been assumed to have importantly shaped aspects of cognitive capabilities in primates (Call & Tomasello 1997; Clutton-Brock & Harvey 1980; Marshall & Wrangham 2007; Milton 1981). For example, feeding ecology influenced performances in an inhibitory control task in two New World monkeys: gummivorous marmosets (*Callithrix jacchus*) out competed closely related, but insectivorous, cotton-top tamarins (*Saguinus oedipus*) in a delayed gratification task. The marmosets waited longer for a larger reward rather than accepting immediate, smaller recompense (Stevens et al. 2005). Conversely, in a spatial discounting task, the tamarins travelled further for greater rewards whereas the marmosets preferred smaller, nearer rewards (Stevens et al. 2005). These behavioural patterns fit the feeding ecology of both species. That is, delayed sap discharge, requiring higher patience in gummivorous marmosets, explains their superior performance in a space-dependent inhibitory control task (Stevenson & Rylands 1988). Insectivorous tamarins, on the other hand, travel larger distances when foraging and, thus, performed better in a time-dependent inhibitory control task (Snowdon & Soini 1988). Similarly, chimpanzees (*Pan troglodytes*), which generally rely on small, distributed food patches and fluctuating fruit resources, showed stronger inhibitory skills in a delayed gratification task than bonobos (*Pan pansicus*) that live in environments with more stable and reliable food sources, suggesting that the different feeding ecologies of chimpanzees and bonobos strongly influence foraging effort and ultimately led to the development of different cognitive abilities (Rosati et al. 2007).

According to the social brain hypothesis evolutionary brain enlargement in group-living mammals was driven by the necessity to develop adequate social manipulation skills, allowing individuals to keep track of complex social relationships (Byrne & Bates 2007). Indeed, comparative analyses revealed positive correlations of mean group sizeand the number of grooming partners with neocortex volume among several mammal species (Barton & Dunbar 1997; Dunbar 1995; Dunbar & Bever 1998; Kudo & Dunbar 2001; Shultz & Dunbar 2006). The neocortex, a part of the mammalian brain, is important for higher cognition (Carlson, 1986) and is suggested to have evolved along with the increasing cognitive requirements of sociality (Dunbar & Shultz 2007; Pérez-Barbería et al. 2007). Comparing seven primate species on five inhibition tasks, Amici et al. (2008) revealed a positive correlation between self-control and the degree of fission-fusion dynamics, the latter being a recognised aspect of social complexity. However, in a larger comparative study, group size, another proxy of social complexity, did not predict performances of 23 primate species in two inhibition tasks (MacLean et al. 2014).

Although studies investigating primate cognition have become more numerous in the last decades, the majority of Old World monkey studies were performed on Cercopithecinae. To this day, knowledge of cognitive capacities in the Colobinae subfamily remains sparse. Here we report the first investigation of inhibitory control skills in endangered red- and grey-shanked douc langurs (*Pygathrix nemaeus* and *P. cinerea*). Red- and grey-shanked doucs are endemic to evergreen and semi-deciduous forests of Indochina. They are diurnal, arboreal and predominantly folivorous, occasionally feeding on seeds, buds, flowers and fruits (Ha Thang Long 2009; Lippold & Vu Ngoc Thanh 2008; Moore & Ali 1984; Nadler 2008; Stevens et al. 2008; Ulibarri 2013; Workman & Covert 2005). Both species live primarily in one-male family groups with on average 13.5 and 8.5 individuals in red- and grey-shanked doucs, respectively (Nadler & Brockman 2014). On a daily basis, one-male units can congregate to larger groups with up to 50 individuals in red-shanked doucs (Lippold 1998) and up to 88 individuals in grey-shanked doucs (Ha Thang Long 2009). These fission-fusion patterns can differ with seasonality (Ha Thang Long 2009; Lippold 1998).

The widespread, temporally stable distribution of the douc langurs' main food source indicates a relaxed feeding competition as is generally assumed in folivorous species (Sterck et al. 1997; Wrangham 1980). This kind of feeding ecology predicts relatively low social skills and high impulsivity. However, their social organisation predicts the opposite. Social skills and self-control are presumably enhanced in group-living primates, particularly those with significant fission-fusion dynamics (Amici et al. 2008; Aureli et al. 2008; Barrett et al. 2003). Aside from the general lack of knowledge on cognition in douc langurs, the contradictory predictions on their self-control skills based on feeding ecology and sociality make them relevant and interesting subjects.

To assess self-control capabilities in red- and grey-shanked douc langurs, we tested 17 captive animals of the Endangered Primate Rescue Center (EPRC) in Vietnam with the cylinder task (MacLean et al. 2013) and the middle-cup task (Call 2001). In the former, subjects are required to perform a detoured side-approach to obtain a reward situated behind a transparent barrier, inhibiting their impulse for a direct frontal approach. In the latter, subjects that observe baiting of two flanking cups must suppress their temptation to pick an empty, central cup. To the best of our knowledge, to date, only one study has investigated inhibitory control in a folivorous colobine species (Tan et al. 2013). In this study, golden snub-nosed monkeys (*Rhinopithecus roxellana*) showed low self-control skills, comparable to those of other folivorous primates (MacLean et al. 2014). Interestingly, their large group sizes and fission-fusion dynamics could not explain poor self-control performances (Tan et al. 2013). Based on these findings, we predict that (I) red- and grey-shanked douc langurs will also show low levels of inhibitory control; and (II) that no differences in self-control skills will occur between both species, as they are closely related and share similar social and ecological environments.

Material and Methods

Study site and subjects

Our study was conducted in the EPRC in Cuc Phuong National Park, Vietnam, from April to June 2015. The park is located in the Nho Quan District of Ninh Binh Province, 120 km south of Hanoi (Wright et al. 2008). The EPRC houses about 160 primates of 15 different Indochinese primate taxa, 4 listed as ‘CriticallyEndangered’, 9 as ‘Endangered’ and 2 as ‘Vulnerable’ (Nadler 2014).

Eight red-shanked douc langurs, including four males (6 to 19 years) and four females (7 to 17 years), and nine grey-shanked douc langurs, with eigh males (6 to 19 years) and one female (6 years), were examined. At the EPRC, animals are housed in chain-link out door enclosures measuring about 10.0 m x 5.5 m x 3.5 m (length x width x height). Enclosures are equipped with natural tree branches and bamboo poles. Douc langurs are provisioned with water ad libitum and fresh leaf bundles three times a day. Additionally, monkeys are provided with pieces of sweet potato once a day.

Experimental design

All primates were completely naïve to cognitive experiments. Experiments took place in the animals’ enclosures. Monkeys were either tested in the morning between 9.30am and 10.30am or in the afternoon between 1.30pm and 2.30pm. During testing, the experimenter and the subject were separated by the enclosure’s mesh. Rewards were offered as small pieces (ca.1 cm x 1 cm) of sweet potato. All animals participated voluntarily in the experiments. If a monkey would not participate in a session, e.g. would not approach the cylinder/sliding table or would not try to receive the reward, the test was terminated and repeated another day.

Cylinder task

In this task, we use the same apparatus and experimental design as suggested in MacLean et al. (2012; 2014).

Apparatus

Two plastic cylinders, one opaque and one transparent, were used in our study. Both cylinders had the same measurements (width = 23 cm, diameter = 13 cm) and were each attached to small wooden boards. The boards were necessary for stabilisation to keep the cylinders from rolling away when manipulated by the animals during the trials.

Procedure

At first, animals were trained to reach for a reward hidden in the centre of an opaque cylinder. The cylinder was baited beyond subject's reach, but the subject could watch the baiting process. The baiting was alternately performed from the right or left side of the cylinder. Afterwards, the cylinder was placed in reach of the monkey so that it could try to retrieve the reward. After successfully conducting five consecutive training trials, subjects were confronted with the experimental transparent cylinder. Test trials were accomplished in the same way as described for the training trials, however, the opaque cylinder was now replaced by the transparent cylinder. A trial was correct if an animal did not attempt to retrieve the reward directly and thereby pushed frontal against the cylinder with its hands. A trial was also rated as successful if an animal clearly used a hand only to pull the cylinder closer in order to secure it for easier access to the sides. Altogether, ten test trials were conducted in this experiment. In both conditions, training and test trials, animals could retrieve the rewards regardless of performance.

Middle-cup task

In this task, we use the same experimental design as proposed in Herrmann et al. (2007) and Amici et al. (2008).

Procedure

Three cups were aligned on a sliding table in front of the animal and two rewards were placed under the two outer cups, while they were out of the monkeys' reach. Afterwards, animals were free to choose among the cups. If the subject chose one of the baited cups it was allowed a second choice. If the animal took the unbaited cup for its first or second choice, the trial was over. A trial was correct, if the monkey chose both baited cups in succession. Altogether, four trials were conducted in this experiment per animal. In this task, animals require self-control to refrain from the tendency of choosing the cup closest to them, which would always be the middle cup.

Data Analysis

All experiments were videotaped. After each trial, the results were announced audibly to the camera and later rechecked when analysing the tapes. Individual success rates were calculated for each inhibitory control task. On the species level, Mann-Whitney U tests were calculated to control for differences in the performances of red- and grey-shanked doucs for both tests. We used Wilcoxon tests to compare individual performances in both tests. The influence of age on monkeys' performances was examined with a Spearman correlation, since age was not normally distributed (Shapiro: $W = .78$, $p < .01$). The same statistical test was used to examine correlations between number of training trials and performance in the cylinder task (Shapiro: $W = .83$, $p < .01$). For both tasks, a second observer scored 24% of test sessions (in total 4 out of 17 sessions per task) to assess inter-observer reliability, which was excellent with an agreement of 100%. All statistical analyses were conducted using R (R Core Team 2014).

Results

In the cylinder task, red- and grey-shanked doucs reached mean success rates of 0.20 ± 0.19 and 0.19 ± 0.25, respectively, and did not differ in their performances (Mann Whitney: $U = 32.5$, $p = 0.77$) (Fig. 1). The number of training trials an individual required before participating in the experimental phase did not correlate with individual's performance in this task (Spearman: $rs = -0.24$, $p = 0.34$).

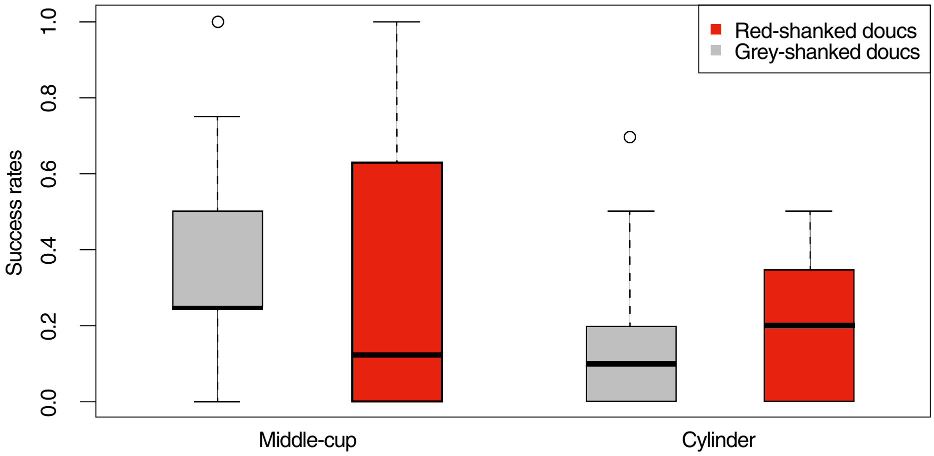

Fig.1. Success rates of red and grey-shanked doucs in the inhibitory control tasks. The bold line across the boxes represents the median. Boxes show the inter-quartile range of scores from the 25th percentile to the 75th percentile. Maximum and minimum values are presented through whiskers and outliers through emty circles.

In the middle-cup task, red-shanked doucs reached a mean success rate of 0.31 ± 0.35 and grey-shanked doucs reached a mean rate of 0.42 ± 0.31. Again no interspecific differences in performances was detected (Mann Whitney U: *U* = 45, *p* = 0.39). Age was not correlated with animals' performances in both experiments (Spearman: cylinder task: *rs* = 0.22, *p* = 0.41; middle-cup task: *rs* = -0.11, *p* = 0.69) (Fig. 2).

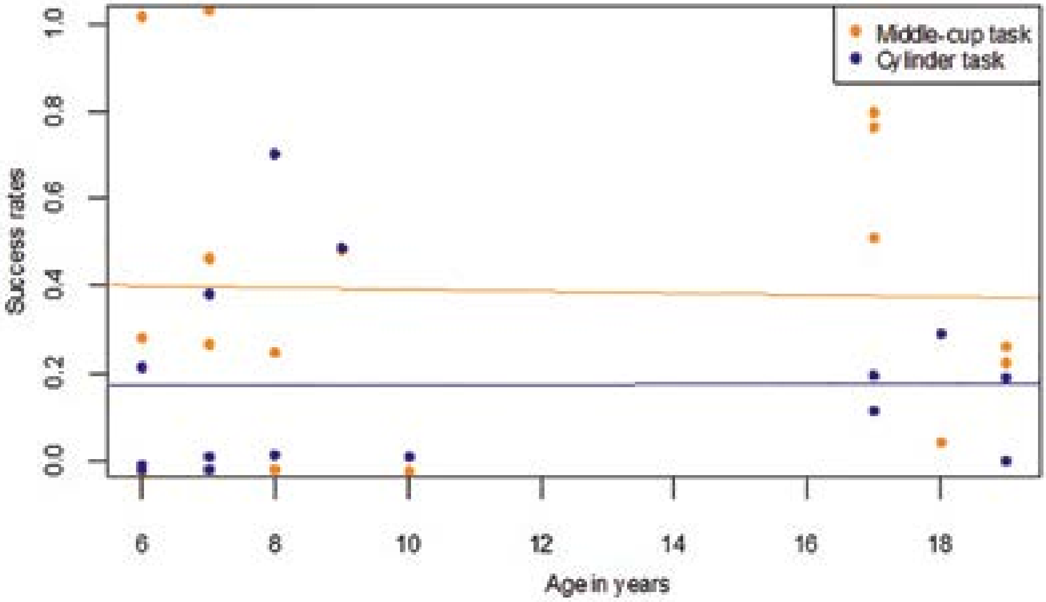

Fig.2. Success rates of all individuals incorrelation to their age in the inhibitory control tasks. In both experiments, no correlation was found between age and performance.

Individual performances did not differ between both experiments (Wilcoxon: *Z* = -1.96, *p*> 0.05).

Discussion

In our study, we present the first data on self-control in red- and grey-shanked douc langurs contributing to the under studied field of cognition in colobines. The two species demonstrate similar low levels of inhibitory control in both tasks. In comparison to other primates (MacLean et al. 2014), they exhibit rather low levels of inhibitory control, which are nevertheless comparable to those of other folivorous primates. Age did not influence animals' performance and individuals did not differ in their scores between both tasks. Interestingly, in the cylinder task red- and grey-shanked doucs scored below all so far tested bird and mammal species. Altogether, since langurs are folivorous our results support the increasing body of empirical studies suggesting that feeding ecology strongly influences inhibitory control skills.

Our findings also indicate that group size and fission-fusion dynamics do not appear to have a strong influence on the development of this cognitive skill. Both species live in groups which regularly split and reassemble - a social system which is commonly regarded as cognitively demanding, including complex interactions and behaviours such as competition and cooperation among conspecifics, frequent monitoring of group movements and tracking of group members (Dunbar 2009). Yet, these demands neither led to the acquisition of enhanced self-control in douc langurs nor in golden snub-nosed monkeys, which share a similar social system (Kirkpatrick & Grueter 2010). For the latter, Tan et al. (2013) posit that their loose associations in assembled groups and rare inter-unit interactions represent a specific type of fission-fusion dynamics that does not require enhanced inhibitory skills. This would also explain douc langurs' poor self-control. In comparison to species of the Cercopithecinae, colobine species like red- and grey shanked douc langurs exhibit rather low levels of social interactions, i.e. grooming or aggression, in their daily activity patterns (Kavanagh 1978; Oates & Davies 1994; Poirier 1974). Furthermore, red- and black-shanked doucs seemingly lack female dominance hierarchies (Rawson 2009; Ruempler 1998). Detecting and understanding social hierarchies, however, constitutes an important cognitive capability and its presence has been suggested to increase social complexity (MacLean et al. 2008). Moreover, the fact that douc langurs regularly congregate to large groups, is contradictory to the assumption that self-control increases with group size and degree of fission-fusion (Amici et al. 2008). Also, in the majority of studies investigating inhibitory control in primates, other mammal species and birds, larger group sizes and frequent fission-fusion dynamics were not linked to increased self-control (MacLean et al. 2014; Stevens 2014; Tan et al. 2013; Vernouillet et al. 2016).With our study we contribute to this literature, as group size and fission-fusion dynamics can not explain douc langurs' poor self-control. The intensity of social interactions within and between groups appears more important for the development of this cognitive skill than group composition.

Feeding ecology seems to be a better predictor for inhibitory skills than social complexity. Douc langurs' poor results in the two self-control tasks align with the low performances of other folivorous primates in the same or similar experiments, e.g. for the cylinder task: Coquerel's sifakas (*Propithecus coquereli*), 36% (MacLean et al. 2014) and golden snub-nosed monkeys, 35% (Tan et al. 2013); for the middle-cup and plexiglas hole task: gorillas (*Gorilla gorilla*), 21% and 42%, respectively (Amici et al. 2008).The reliance on food sources that are spatially and temporally highly abundant and easy to harvest unlikely engenders inter- and intragroup competition (Isbell & Young 1993; 2002; Sterck et al. 1997; Wrangham 1980). Additionally, leaf-eating does not demand complex foraging strategies where animals have to show patience, e.g. gummivores waiting for gum to exudate or carnivores stalking on their prey, or temporal and spatial orientation, e.g. frugivores which need to know about the maturing of fruits and the position of fruit trees.

However, dietetic categorisations of primate species as "pure" folivores, frugivores or gummivores have been recently criticised (Sayers 2012) and should be treated with caution. For example, most folivorous primates include small amounts of fruits, seeds or flowers in their diets. For harvesting these different food types other feeding strategies and cognitive abilities are required. Furthermore, many studies have identified folivores as very selective feeders primarily foraging high-quality foods that are often temporally and spatially dispersed (Chapman et al. 2003; Glander 1982; Kirkpatrick 1999; Oates 1994; Snaith & Chapman 2007; Yeager & Kool 2000). Thus, the cognitive demands of a folivorous species might be therefore more complex than formerly assumed. Nevertheless, our results contribute to the empirical body of literature suggesting that folivorous species possess lower self-control than species with other main food sources, and that inhibitory capacities highly depend on a species' feeding ecology.

Strikingly, in the cylinder task, douc langurs did not just reveal poor inhibitory skills but they also scored below all 31 tested mammal and bird species examined in the study by Maclean et al. (2014). As all of our individuals successfully passed a training phase with an opaque cylinder, a general lack of understanding how to retrieve the rewards can be excluded. Moreover, the number of training trials subjects required to advance to the testing trials did not predict the outcome. Hence, douc langurs' errors in the cylinder task may have been driven by their principal lack of self-control. Yet, although douc langurs' feeding ecology predicts low levels of self-control, their performance was even outcompeted by another colobine species, the golden snub-nosed monkeys which share a similar ecological environment but scored almost twice as high in the same task (Tan et al. 2013). Since golden snub-nosed monkeys have larger brains then douc langurs (Isler et al. 2008) and absolute brain size predicted performance in self-control tasks across primates (MacLean et al. 2014), the combination of both factors may explain the difference in performance between these species.

Conclusion

This study provides a first insight into inhibitory skills in captive red- and grey-shanked douc langurs in two different tasks. Both species revealed similar low levels of self-control, and, to the best of our knowledge, reached the lowest scores among all tested species in the cylinder task. Their poor self-control skills are in line with the performances of other folivorous primates and suggest that feeding ecology influences performance in this cognitive skill. A large group size and fission-fusion dynamics, both aspects of social complexity, cannot explain douc langurs' performances. Future research on cognition should therefore focus on colobine species, as comparative studies generally lack this important subfamily.

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Distribution of the northern yellow-cheeked gibbon (*Nomascus annamensis*) in Central Vietnam

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Key words: Northern yellow-checked gibbon, vocalisation, distribution

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Summary

The northern yellow-cheeked gibbon (*Nomascus annamensis*) is a species that occurs only in Central Vietnam, southern Laos and northern Cambodia. This species, morphologically similar to the southern yellow-cheeked gibbon (*N. gabriellae*), was recently described by Van Ngoc Thinh et al. (2010) on the basis of genetic and vocal characters. Up to date only a few surveys have been carried out on the species, but information about distribution is essential for its conservation. To obtain further information on the distribution of *N. annamensis*, we recorded gibbon songs in various protected areas, including Bac Huong Hoa Nature Reserve (NR) and Dakrong NR in Quang Tri Province, Phong Dien NR, Bach Ma National Park (NP) and Hue Saola NR in Thua Thien Hue Province, Song Thanh NR in Quang Nam Province, Chu Mom Ray NP in Kon Tum Province and Kon Ka Kinh NP in Gia Lai Province. In total, 171 individuals (73 males, 98 females) in 71 groups were recorded and analyzed in comparison with recordings of *N. siki* and *N. gabriellae*. The data confirm the presence of *N. annamensis* in eight protected areas in central Vietnam: Bac Huong Hoa NR (10 groups), Dakrong NR (7 groups), Phong Dien NR (10 groups), Bach Ma NP (13 groups), Hue Saola NR (8 groups), Song Thanh NR (2 groups), Chu Mom Ray NP (14 groups) and Kon Ka Kinh NP (7 groups).

Sự phân bố của vượn đen má hung trung bộ (*Nomacus annamensis*) tại miền trung Việt Nam

Tóm tắt

Vượn đen má hung trung bộ (*Nomacus annamensis*) là loài đặc hữu của Việt Nam, Lào, Campuchia. Loài này có hình thái tương tự vượn đen má vàng (*N. gabriellae*) được phát hiện bởi Văn Ngọc Thịnh và et al năm 2010 trên cơ sở phân tích di truyền và tiếng hót. Cho đến nay chỉ có một số ít cuộc điều tra về loài được tiến hành, nhưng thông tin về sự phân bố là rất cần thiết cho bảo tồn chúng. Để có thêm thông tin về sự phân bố của (*N. annamensis*), chúng tôi tiến hành ghi nhận bài hát vượn trong khu vực bảo vệ khác nhau bao gồm: Khu bảo tồn thiên nhiên (KBTTN) Bắc Hướng Hóa và Đakrông , tỉnh Quảng Trị; KBTTN Phong Điền , Vườn quốc gia (VQG) Bạch Mã, KBTTN Sao La Thừa Thiên Huế, tỉnh Thừa Thiên Huế; KBTTN Sông Thanh, tỉnh Quảng Nam; VQG Chư Mom Ray , tỉnh Kon Tum; VQG Kon Ka Kinh tỉnh Gia Lai. Kết quả khảo sát tại trung bộ, Việt Nam đã ghi nhận được 171 cá thể trưởng thành (73 đực, 98 cái) trong 71 đàn đã được ghi nhận và phân tích so sánh với các bản ghi âm của *N. siki* và *N. gabriellae*. Các dữ liệu xác nhận sự hiện diện của *N. annamensis* trong tám khu bảo tồn ở Trung Bộ Việt Nam: KBTTN Bắc Hướng Hóa (10 đàn) , KBTTN Đakrông (7 đàn) , KBTTN Phong Điền (10 đàn) , VQG Bạch Mã (13 đàn) , Khu bảo tồn Sao La Huế (8 đàn), KBTTN Sông Thanh (2 đàn), VQG Chư Mom Ray (14 đàn) và VQG Kon Ka Kinh (7 đàn).

Introduction

The Central Annamite mountain range of Vietnam is one of the country's biodiversity hotspots and of worldwide importance identified by WWF 200 global priority ecosystem. The region is habitat for many rare and endemic species including the recently rediscovered for the first time after 15 years saola (*Pseudoryx nghetinhensis*), giant muntjac (*Muntiacus vuquangensis*), Truong Son muntjac (*Muntiacus truongsonensis*), grey-shanked douc langur (*Pygathryx cinerea*), red-shanked douc langur (*Pygathrix nemaeus*), Asian elephant (*Elephas maximus*) as well as the northern yellow-cheeked gibbon (*Nomascus annamensis*).

The northern yellow-cheeked gibbon (Fig. 1) was described as a new species (Van Ngoc Thinh et al. 2010a). Although *N. annamensis* is similar to the southern yellow-cheeked gibbon (*N. gabriellae*) in external appearance, both species clearly differ in their vocalisation and mitochondrial DNA (Konrad & Geissmann 2006; Rawson et al. 2011; Van Ngoc Thinh 2010; Van Ngoc Thinh et al. 2010a; 2010b; 2010c; 2011). Although the general distribution of *N. annamensis* in southern Laos, North Cambodia and Central Vietnam is well known, detailed information about the exact distribution range and occurrence in protected areas, as well as estimates of population sizes are lacking.

Fig.1. Left: Southern yellow-cheeked gibbon (*Nomascus gabriellae*); Right: Northern yellow-cheeked gibbon (*Nomascus annamensis*) – males above, females below. The coloration of these species is very similar and the species is not to identified in the field. Photos: Tilo Nadler.

Similar to the other crested gibbon species, *N. annamensis* is threatened by illegal hunting, habitat loss due to illegal logging, forest conversion into agricultural land and plantations, and for the construction of roads and hydropower stations.

To overcome these limitations, we conducted field surveys in eight protected areas in Central Vietnam and recorded gibbon songs with the aim to confirm the presence of the species and to estimate its population size and group composition.

Methods

Survey areas

The herein presented acoustic data is a combination of those collected by Van Ngoc Thinh during a period from 2009 to 2011 (Van Ngoc Thinh 2010) and data newly collected in 2012. In total, eight protected areas were selected as survey areas. These are Huong Hoa NR and Dakrong NR (Quang Tri Province), Phong Dien NR, Hue Saola NR and Bach Ma NP (Thua Thien Hue Province), Song Thanh NR (Quang Nam Province), Chu Mom Ray NP (Kon Tum Province) and Kon Ka Kinh NP (Gia Lai Province) (Fig. 2.).

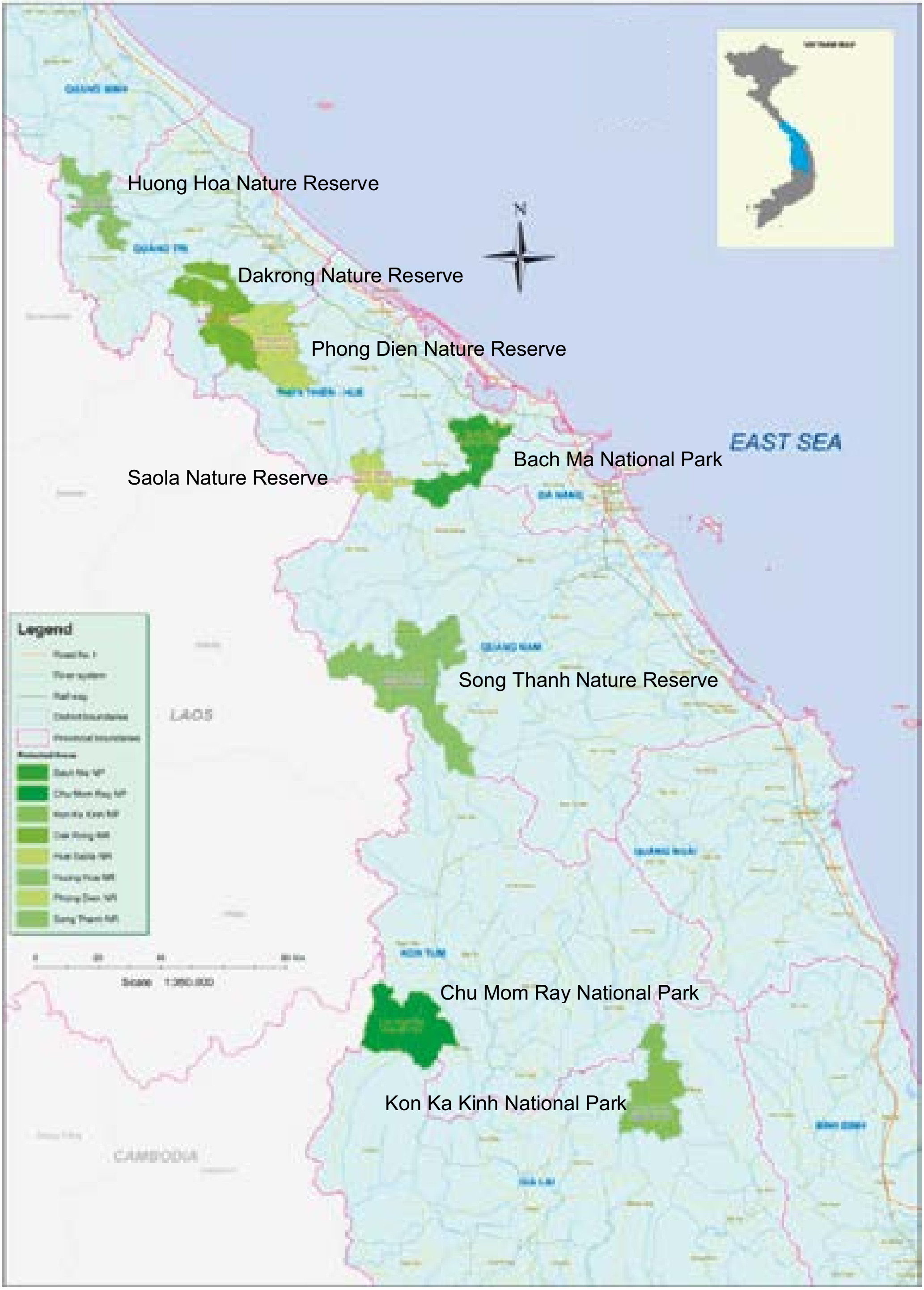

Fig.2. The eight protected areas where surveys conducted.

Data collection

Before we conducted surveys in the forest, we collected information about the occurrence of *N. annamensis* by interviewing local people and rangers who frequently access the forest. Based on this information, we selected mountain peaks as listening posts, since only on the peak of high mountains; gibbon vocalisation coming from different directions surrounding the area can be recorded. Survey groups recorded gibbon songs at the listening posts from 5:00am to 9:00am. After that, they surveyed along existing trails ('transects') for direct observations of groups or individuals in the surrounding areas until 2:00 to 3:00pm. Surveyors walked slowly on the routes. Noise and smoking were prohibited during transect surveys in order to maximize observations by reducing disturbance. Sometimes, surveyors stopped to listen to gibbon calls or due to gibbon movement. When gibbon songs were heard close by, the surveyors approached quietly to record the voice by a digital recorder, and to verify the exact size and composition of the group.

In eight protected areas, 33 positions were set to perform recording. In average, 2-6 positions were chosen to record. When the gibbon song was listened surrounding the set position, the micro would be turn to the voice source direction to assure that the clearest sound was recorded. In case that two groups of gibbons were singing at the same time and same position, they were recorded one after the other.

While recording gibbon songs, we documented also other information including: position, azimuth, distance (estimated) from sound source to listening position (upon practical experience and measuring on map), recorder, recording date, starting and ending point of gibbon song recorded, song types, group number (depends on song), individual number, sex, age sections also taken note into a form.

Methods for gibbon song vocal analysis

Recorded sound data were analysed by using Avisoft SASLab Pro software. The analytic process was performed as follows:

- Convert sound data file obtained in the field to a typical format as WAV.
- Launching Avisoft – SASLab Pro software.
- Running the program and analysis.

Acoustic analysis of the sound sonograms of northern yellow-cheeked gibbon shows the differences in the vocalization of mature males and females (Fig. 3). The male gibbon song is shorter, more regular and belongs to a band from 1 to 2 kHz, while the female gibbon song is longer, with larger amplitude from 0.5 to 3 kHz. Females produce fast up-down sweeps like a spiral spring, with a vibrato sound on the first two notes. Males produce staccato sounds during, before and after their multi-modulated phrases. All male songs start with almost unmodulated frequency, followed by a down sweep and a fast up sweep. Accordingly, differences in male and female gibbon songs of mature individuals can be easily determined.

Results

In total 30,853 seconds of gibbon songs were recorded, of which 337 were from gibbon couples and 831 from solo males. At least 171 individuals of northern yellow-cheeked gibbons could be indentifyed - 73 males and 98 females - which leads to an estimation of 71 groups in total at the 8 protected areas (Table 1).

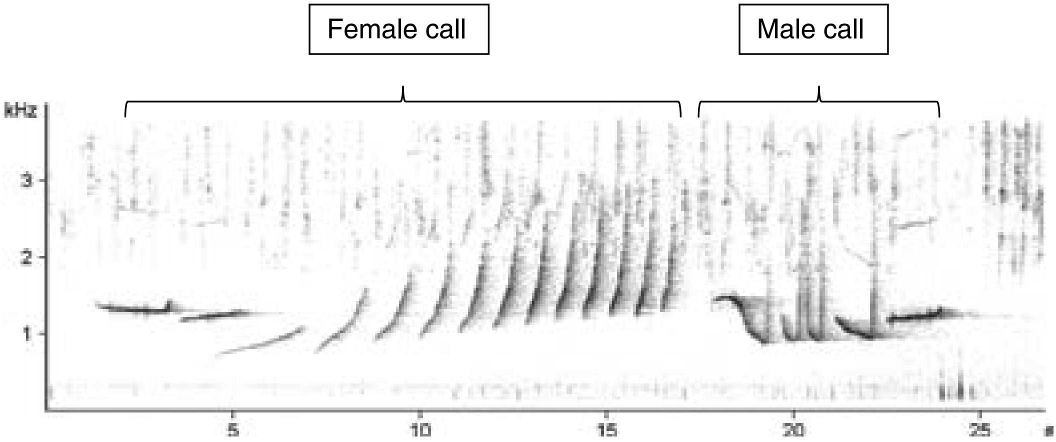

Fig.3. Differences between male and female gibbons songs of the northern yellow-cheeked gibbon in a sound spectrogram.

Table 1. Summary of the acoustic analysis with information about group size, group composition and duration time of recorded songs in the eight surveyed protected areas.

	Number of					
Locality	**Groups**	**Duet calls**	**Male solo calls**	**Males**	**Females**	**Duration of recorded songs in sec.**
Huong Hoa Nature Reserve	10	47	71	10	16	3,550
Dakrong Nature Reserve	7	41	92	7	8	2,920
Phong Dien Nature Reserve	10	44	127	10	14	2,944
Saola Nature Reserve	8	30	185	8	9	4,669
Bach Ma National Park	13	44	137	15	19	4,046
Song Thanh Nature Reserve	2	5	14	2	3	460
Chu Mom Ray National Park	14	106	122	14	18	7,612
Kon Ka Kinh National Park	7	60	83	7	11	4,652
Total	71	377	831	73	98	30,853

Acknowledgements

We would like to thank WWF-Vietnam, the Management Board of Bach Ma, Chu Mom Ray and Kon Ka Kinh National Parks, and Huong Hoa, Dakrong, Phong Dien, Hue Saola, and Song Thanh Nature Reserves for their kindly support, providing information and staff to join the survey team. We are also grateful to the staff and rangers of these protected areas for their supports and their participation. In addition, we would like to thank local communities for providing information during the interviews and local guides who supported the survey team during the surveys.

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The Vietnam Primate Conservation Program – Report 2016

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Key words: Endangered Primate Rescue Center, Vietnam, primate conservation

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Summary

For the five years period 2014 – 2018 the Vietnam Primate Conservation Program continues its work in partnership with Zoo Leipzig, Germany. The content of the project, approved by the Ministry of Agriculture and Rural Development includes two main parts, the maintenance of the Endangered Primate Rescue Center and conservation work outside of the EPRC with reintroduction of animals to restock or reintroduce wild populations and primate conservation activities in protected areas.

Mr. Do Van Lap Vicedirector of Cuc Phuong National Park holds also the position as Director of of the Vietnam Primate Conservation Program assisted by Tilo Nadler as Co-Director of the Program. Responsible for the management of the EPRC is the new managing Director Sonya Prosser, also appointed as representative of Leipzig Zoo in Vietnam.

With beginning of 2015 these parts of the Primate Conservation Program are shared between Sonya Prosser as new managing Director of the EPRC and representative of Leipzig Zoo in Vietnam, and Tilo Nadler, as Co-Director of the program for the conservation work outside of the EPRC.

End of 2016 the EPRC kept 164 primates and received during the year the highest number of rescues in its history, with a total of 35 animals. Fifteen animals of 8 species were born. The total staff of the Vietnam Primate Conservation Program counts now 34 (29 animals keepers, 1 project assistant, 1 project coordinator, 1 foreign head keeper, 1 managing Director of the EPRC and 1 Co-Director of the Program). Staff members participated in training courses and study tours. An education program for children was developed and staff from the EPRC collaborated with the ‘Conservation Awareness Program’ team from Cuc Phuong National Park. One master student from the Central Washington University, US collected data on douc langurs at the semi-wild area for a master thesis.

During the year 1442 Vietnamese and 3813 foreigners visited the EPRC.

Under the Primate Conservation Program two reintroduction programs continued: the reintroduction of pygmy loris (*Nycticebus pygmaeus*) and Bengal slow loris (*N. bengalensis*) into Cuc Phuong National Park and Hatinh langurs (*Trachypithecus hatinhensis*) into Ke Go Nature Resere, Hatinh Province. In total 10 pygmy lorises and 4 Bengal slow lorises were released into Cuc Phuong National Park. The animals were equipped with radio collars and tracked daily to collect information about their movement and habitat use.

Mid June 2015 a first group of captive bred Hatinh langurs was released into Ke Go Nature Reserve. The released animals adapted well to the natural environment, and showed a natural behaviour. But a completely unexepcted attack of this group by a very large and agrressive macaque band (*Macaca mulatta*) split the group, caused the death of some langurs and interrupted the continuation of the release. In July 2016 a second group was released. The animals were equipped with satellite radio collars and tracked daily until end of 2016.

The support for protection and management of Van Long Nature Reserve continues and funds were raised to cover the costs for the work of the ‘Community based Protection Unit’ and to implement the SMART-Patrol Program through providing GPS units, computer and a one week training course for the guards and rangers. The financing was generously provided by “The Thin Green Line” and FOUR PAWS-VIET.

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Chương trình Bảo tồn Linh trưởng Việt Nam – Báo cáo năm 2016

Tóm tắt

Trong giai đoạn 5 năm 2014 – 2018 Chương trình Bảo tồn Linh trưởng Việt Nam tiếp tục thực hiện và được hợp tác với Vườn thú Leipzig, CHLB Đức. Nội dung của dự án được Bộ Nông nghiệp và Phát triển Nông thôn phê duyệt gồm hai hợp phần chính là vận hành Trung tâm Cứu hộ Linh trưởng Nguy cấp (EPRC) và hoạt động bảo tồn bên ngoài EPRC như tái hòa nhập động vật nhằm tăng viện số lượng còn ngoài tự nhiên hay tái thả các cá thể được cứu hộ từ hoang dã và hoạt động bảo tồn linh trưởng tại các vườn quốc gia và khu bảo tồn. Ông Đỗ Văn Lập, Phó Giám đốc Vườn Quốc gia Cúc Phương vẫn giữ cương vị Giám đốc Dự án Chương trình Bảo tồn Linh trưởng Việt Nam với sự hỗ trợ của ông Tilo Nadler vẫn giữ cương vị Đồng Giám đốc Dự án. Chịu trách nhiệm quản lý EPRC là bà Sonya Prosser, Giám đốc điều hành, đồng thời cũng giữ cương vị là Đại diện của Vườn thú Leipzig tại Việt Nam.

Đến cuối năm 2016, EPRC đã chăm sóc cứu hộ 164 cá thể linh trưởng và số lượng động vật được cứu hộ đã tăng đột biến với số lượng cao nhất trong lịch sử cứu hộ, tổng cộng 35 cá thể. 15 cá thể thuộc 8 loài được sinh mới. Cán bộ, nhân viên và chuyên gia của dự án bao gồm 34 lao động: 29 nhân viên chăn nuôi thú, 1 trợ lý Dự án, 1 điều phối viên Dự án, 1 chuyên gia phụ trách chăn nuôi, 1 Giám đốc điều hành EPRC và Đồng Giám đốc Dự án Chương trình Bảo tồn Linh trưởng Việt Nam. Nhân viên tham gia vào các khoá tập huấn chuyên môn ngắn hạn và thăm quan học tập. Một chương trình giáo dục cho trẻ em mới được triển khai, nhân viên của EPRC phối hợp với Nhóm nâng cao nhận thức bảo tồn thuộc Vườn Quốc gia Cúc Phương. Một sinh viên cao học đến từ Đại học Central Washington, Hoa Kỳ đã thực hiện đề tài thu thập dữ liệu về voọc Chà vá chân xám trong khu vực bán hoang dã cho luận văn tốt nghiệp.

Trong năm vừa qua đã có 1442 lượt du khách Việt Nam và 3813 lượt du khách nước ngoài tới thăm EPRC.

Hợp phần hai của Chương trình Bảo tồn Linh trưởng Việt Nam là tái hòa nhập linh trưởng đã được tiếp tục thực hiện: tái thả loài cu li nhỏ (*Nycticebus pygmaeus*) và loài cu li lớn (*N. bengalensis*) tại Vườn Quốc gia Cúc Phương và voọc Hà Tĩnh (*Trachypithecus hatinhensis*) tại Khu bảo tồn thiên nhiên Kẻ Gỗ, tỉnh Hà Tĩnh. Tổng số 10 cá thể cu li nhỏ và 4 cá thể cu li lớn được trở về tự nhiên tại Vườn Quốc gia Cúc Phương. Các cá thể được đeo chip là thiết bị định vị và theo dõi hàng ngày nhằm thu thập số liệu về sự di chuyển, sinh tồn và tái hòa nhập trong môi trường sống tự nhiên.

Giữa tháng 6 năm 2015, những cá thể đầu tiên của voọc Hà Tĩnh đã sinh trưởng trong điều kiện nuôi nhốt đã được tái hòa nhập trở về tự nhiên tại Khu bảo tồn thiên nhiên Kẻ Gỗ. Các cá thể được hòa nhập trở vệ tự nhiên đã thích nghi tốt với môi trường sống ngoài hoang dã và thể hiện nhiều hành vi tập tính tự nhiên. Nhưng đã xẩy ra sự việc không lường trước là đàn voọc đã bị một đàn khỉ vàng (*Macaca mulatta*) khá lớn và hung dữ tấn công dẫn đến thiệt mạng cho 2 cá thể cái và hai cá thể con bé, do vậy quá trình theo dõi tái thả đã bị giãn đoạn vào tháng cuối năm. Tháng 7 năm 2016, đàn voọc thứ hai được tái thả, động vật cũng được đeo thiết bị định vị và được theo dõi đến hết năm 2016.

Tiếp tục tài trợ kinh phí và cố vấn kỹ thuật cho công tác bảo vệ rừng cộng đồng tại Khu bảo tồn thiên nhiên đất ngập nước Vân Long tỉnh Ninh Bình. Chương trình tuần tra kiểm soát rừng bằng chương trình SMART-Patrol thông qua việc cung cấp máy định vị GPS, một bộ máy tính bàn và khoá tập huấn trong một tuần về vận hành thiết bị cho nhân viên bảo vệ và kiểm lâm. Kinh phí tài trợ Vân Long được gây quỹ từ tổ chức “The Thin Green Line” và FOUR PAWS Viet.

Introduction

For the five years period 2014 – 2018 the Vietnam Primate Conservation Program continues its work in partnership with Zoo Leipzig, Germany. The content of the project, approved by the Ministry of Agriculture and Rural Development includes two main parts:

1. the maintenance of the Endangered Primate Rescue Center which focuses on the confiscation of threatened primates from the illegal wildlife trade in cooperation with Forest Protection Authorities, the housing and rehabilition of these individuals, the establishment and maintenance of captive populations of selected ‘Endangered’ and ‘Critically Endangered’ species and

2. conservation work outside of the EPRC with reintroduction of animals to restock or reintroduce wild populations and primate conservation activities in protected areas.

With beginning of 2015 these parts of the Primate Conservation Program are shared between Sonya Prosser as new managing Director of the EPRC and representative of Leipzig Zoo In Vietnam, and Tilo Nadler who keeps the position as Co-Director of the Primate Conservation Program in cooperation with the Vietnamese Director of the Program Mr. Do Van Lap, also Vice Director of Cuc Phuong National Park. The two parts of the Primate Conservation Program, the management of the Endangered Primate Rescue Center and primate conservation work outside of the center are now divided and separately manned.

1. Endangered Primate Rescue Center

1.1. Animals at the EPRC

End of 2016 the EPRC kept 164 primates (Table 1). During this year the EPRC received the highest number of rescues in its history, with a total of 35 animals. Of these, 13 animals were infants requiring additional care (Table 2).

Table 1. Primate collection at the EPRC December 2016.

No.	Species	IUCN Status	Number of individuals
1	*Trachypithecus delacouri*	Critically Endangered	16
2	*Trachypithecus hatinhensis*	Endangered	41
3	*Trachypithecus francoisi*	Endangered	4
4	*Trachypithecus laotum*	Vulnerable	1
5	*Trachypithecus crepusculus*	Endangered	4
6	*Pygathrix nemaeus*	Endangered	12
7	*Pygathrix cinerea*	Critically Endangered	39
8	*P. nemaeus x T. hatinhensis*	-	1
9	*Nomascus gabriellae*	Endangered	3
10	*Nomascus siki*	Endangered	9
11	*Nomascus annamensis*	Not Evaluated	6
12	*Nomascus leucogenys*	Critically Endangered	4
13	*Nycticebus bengalensis*	Vulnerable	14
14	*Nycticebus pygmaeus*	Vulnerable	10
	Total		164

Table 2. Incoming and outgoing animals at the EPRC 2016.

Species	Rescue	Birth	Death	Release	Transfer
Trachypithecus delacouri	0	2	0	0	0
Trachypithecus hatinhensis	0	1	4	4	8
Trachypithecus francoisi	0	1	0	0	0
Trachypithecus crepusculus	0	0	0	0	0
Pygathrix nemaeus	2	2	6	0	6
Pygathrix cinerea	2	5	3	0	3
Pygathrix nigripes	3	0	3	0	3
P.nemaeus x T.hatinhensis	0	0	0	0	0
Nomascus gabriellae	0	0	0	0	0
Nomascus siki	1	2	2	0	2
Nomascus annamensis	3	1	0	0	0
Nomascus leucogenys	1	0	0	0	0
Nycticebus bengalensis	11	1	7	4	12
Nycticebus pygmaeus	12	0	4	1	6
Total	**35**	**15**	**29**	**9**	**40**

The Delacour's langur group in the semi-wild enclosure "Hill 1" produced two offspring, both healthy and active. There was one Hatinh langur born, as most Hatinh langur females still have young from previous years. The grey-shanked douc langurs produced 5 offspring from 4 family groups. Of the grey-shanked and red-shanked douc langurs born, two had to be hand-raised due to near fatal attacks by the father (Fig. 1).

One male Francois langur was born to our only group, the last animal being born in 2011.

Four Hatinhlangurs were released to Ke Go Nature Reserve, beginning with one male and two females. An additional male was released in December. Four Bengal slow lorises and one pygmy loris were released into Cuc Phuong National Park throughout the year.

One Bengal slow loris and one pygmy loris, unsuitable for release, were transferred to Hanoi Zoo.

Fig.1. Hand raising of two confiscated douc langurs and two douc langurs which had to be hand-raised due to near fatal attacks by the father. Photo: Tilo Nadler.

Four Hatinh langurs and one red-shanked douc langur died as a result of complications related to old age. One infant red-shanked douc died one day after arriving at the EPRC due to being too weak for successful rescue, and three lorises also died due to their bad condition when arriving to the EPRC.

Three infant black-shanked douc langurs and one infant grey-shanked douc langur died from an unknown illness that affected all four animals. The animals were unsuccessfully treated, and immediate post-mortems were performed on all. Results from diagnostics are pending. One infant grey-shanked douc langur that displayed the same symptoms has since been successfully treated, and shows no further deterioration. All other deceased animals died from unknown, but unrelated causes.

1.2. Staff at the EPRC

With beginning of 2015 Sonya Prosser took over the management of the EPRC as new Director from Tilo Nadler who held this position since establishment of the center in 1993 for 22 years. Tilo Nadler keeps his position as Co-Director of the Vietnam Primate Conservation Program

The position of Nguyen Thi Thu Hien as project coordinator for the EPRC has been phased out end of the year and she will work under Tilo's management for the project parts outside of the EPRC.

Elke Schwierz continued in her position as head animal keeper and manages and supervises the daily work at the EPRC in cooperation with the Vietnamese head keepers Nguyen Thu Hue and Ding Van Vinh.

The project assistent Nguyen Trung Hieu left the EPRC after completion of a one year contract and Miss Pham Thi Thu Ly took over this role in December 2016.

In the collective of animal keepers were several replacements and the total staff of the EPRC counts now 29.

Additional to the permanent staff 22 volunteers supported the EPRC during the year in various ways.

1.3. Training and capacity building for EPRC staff

Nguyen Thu Hue, Do Dang Khoa and Sonya Prosser attended a one day workshop in Hanoi where participants shared knowledge and experience related to the conservation of loris species in Vietnam.

All staff of EPRC took part in a day trip to Bao Son Safari Park. This trip aimed to reward staff with new experiences and encourage to learn about wild animals, their care and conservation.

Three animal keepers and the head keeper Elke Schwierz travelled to Singapore Zoo for a week long study tour.

Do Dang Khoa visited Cat Tien National Park to assisst in loris release undertaken by the Dao Tien Endangered Primate Species Centre.

A keeper training booklet (Fig. 2) was produced, designed to assist staff in improving their animal care skills.

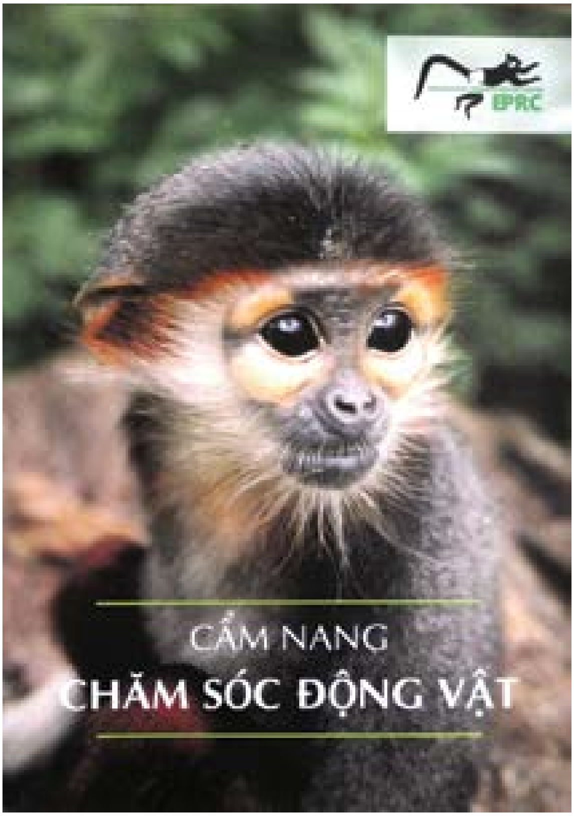

Fig.2. A keeper training booklet was produced designed to assist staff in improving their animal care skills.

1.4. Education

Staff from the EPRC collaborated with the 'Conservation Awareness Program' team from Cuc Phuong National Park to organize field trips for 60 students from 2 schools in the surrounding area of the national park.

An education program for children was developed and the students from local schools were invited to the EPRC to get information about wildlife and necessary conservation activities in Vietnam (Fig. 3).

Fig.3. The education program invited children form surrounding schools of the national park to a visit of the EPRC. Photo: Elke Schwierz.

The EPRC continued the cooperation with Frankfurt Zoological Society and Danang University to deliver lectures on the annualy organized primate training courses at Danang University, and Tilo Nadler and Sonya Prosser gave presentations.

In September Tilo Nadler lectured in a training course on wildlife species identification, organized by the Wildlife Conservation Society to train officers from the Center for Criminology and Crime Investigation, Anti-smuggling Police Department, Environmental Police Department and judicial officers

On a training course 'Conservation Gentics' at Hanoi National University, organized by the American Museum of Natural History, the Centre for Natural Resources and Environmental Studies and the German Primate Center Tilo Nadler lectured about the wildlife trade problems in Vietnam.

1.5. Participation in workshops and conferences

In September Tilo Nadler was invited to a consultation workshop on the law on forest protection and development organized by VN Forest of the Ministry of Agriculture and Rural Development.

In October/November Tilo Nadler and Sonya Prosser attended the 8th WARN-Conference in Hua Hin, Thailand and Tilo Nadler delivered a presentation 'Primate Reintroduction - Experiences and Challenges'. WARN, the Wild Animal Rescue Network is an international organization registered in the Netherlands and devoted to the rescue, rehabilitation and conservation of wildlife. About 25 rescue and rehabiltation centers in 12 Southeast Asian countries are involved (Fig. 4). Tilo Nadler is one of the founders and a board memeber of the organization.

Fig.4. The audience of the 8th annual WARN-Conference in Hua Hin, Thailand. Photo: Tilo Nadler.

1.6. Scientific research

The master student Hilary Hemmes-Kavanaugh observed the group of grey-shanked douc langurs at the semi-wild enclosure to collect behavioural data for her master thesis at the Central Washington University.

1.7. Visitors at the EPRC

During the year 1442 Vietnamese and 3813 foreigners visited the EPRC, managed from guides of the national park.

2. Reintroduction of primates and conservation activities

2.1. Reintroduction of pygmy and slow lorises (*Nycticebus pygmaeus, N. bengalensis*)

The EPRC receives a constant flow of confiscated lorises from the illegal wildlife trade. With the high number of animals, guidelines and recommendations for a release back into the wild are necessary to ensure their survival in the wild after release. A reintroduction project was designed as a pilot study to collect data and to obtain basic information about suitable habitats, appropriate season for release, home range size and activities of pygmy lorises.

The project was carried out in cooperation with the PhD student Stefanie Poindexter from Oxford Brooks University, an institution which is deeply involved in loris studies, and the master student Giannina Reiser from University Braunschweig, Germany.

In total 10 pygmy lorises (5 males; 5 females – one in 2016) and four Bengal slow lorises (1 male; 3 females) were released into Cuc Phuong National Park. The animals were fitted with radio collars and tracked daily to collect information about their movement and habitat use (Fig. 5).

Fig.5. Release of a radio collared Bengal slow loris into Cuc Phuong National Park. Photo: Tilo Nadler.

The results of the project provide information about necessary habitat structure, home range pattern, daily and seasonal activities of both lorises' species.

2.2. Reintroduction of Hatinh langurs (*Trachypithecus hatinhensis*)

A reintroduction project for Hatinh langurs was carried out at Ke Go Nature Reserve, Hatinh Province. Mid June 2015 the first group Hatinh langurs comprising 5 captive bred individuals (1 adult male, 2 adult femals, 2 subadult females) was released.

The released animals adapted well to the natural environment, and showed a natural behaviour. But a completely unexepcted attack on this group by a very large and agrressive macaque band (*Macaca mulatta*) split the group, caused the death of some of the released langurs and interrupted the continuation of the release.

In July 2016 a second attempt was made with the reintroduction of three Hatinh langurs (1 adult male, 2 adult females) at a new location - a peninsula in the Ke Go Lake - to avoid confrontation with macaques (Fig. 6). After one and a half months the langurs moved out from the peninsula to the main area of the nature reserve. Due to malfunction of the males radio collar it could not found and data download was not possible anymore.

Fig.6. The Hatinh langurs in a temporary cage after transportation from the Endangered Primate Rescue Center and prior to release. Photo: Tilo Nadler.

To support the establishment of a group in December 2016 another adult male from the EPRC was released close to one of the females (Fig. 7, 8).

Fig.7. To reach the release site of the Hatinh langurs, staff first needed to carry them for a 2 hours trek through the dense forest. Photo: Tilo Nadler.

Fig.8. The release site chosen for the male was at the top of a hill, close to a previously released female. Photo: Tilo Nadler.

The monitoring of the released individuals was carried out from biologists of the Vietnamese NGO "Green Viet" together with rangers of the nature reserve.

An extraordinary high flooding in the whole province also flooded the research camp and caused difficulties for the monitoring (Fig. 9). A very simple field station was established to continue with the monitoring for several weeks (Fig. 10.), and enabled the data download of the coordinates from released individuals for further analysis and evaluation (Fig. 11).

Fig.9. Extraordinary high flooding in the whole province, also flooded the research camp and the monitoring team had to move. Photo: Bui Duc Huy.

Fig.10. After the flooding a field camp was established to continue with the monitoring an the data download from the radio collars. Photo: Tilo Nadler.

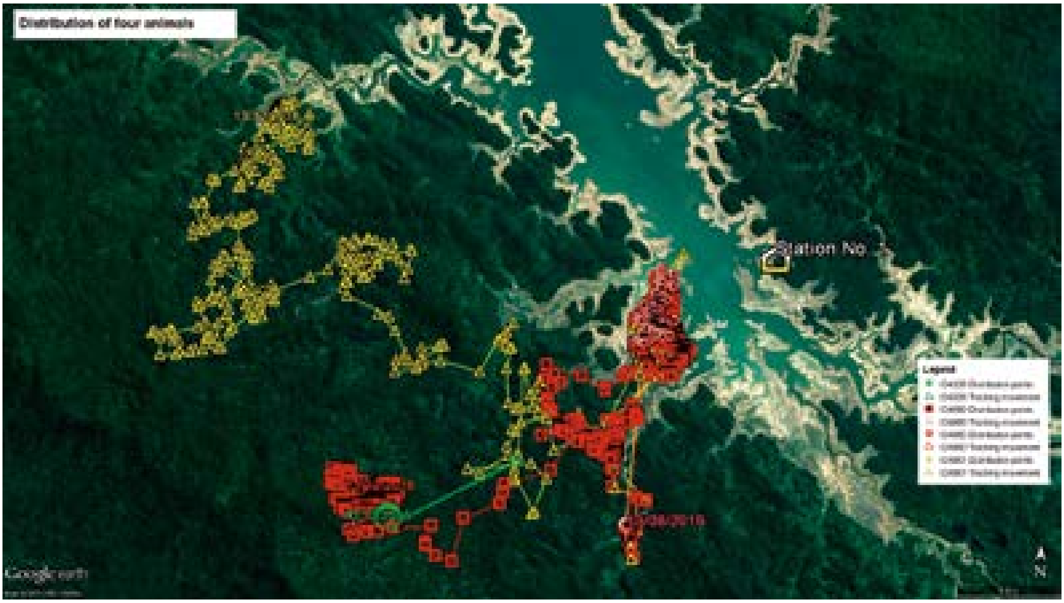

Fig.11. The data from the radio collars allow an analysis of the travel, habitat use and home ranges of the released langurs.

2.3. Conservation and protection activities in Van Long Nature Reserve

The protection of Van Long Nature Reserve, the area which holds the only viable population of the ‘Critically Endangered’ Delacour’s langur was supported and supervised by the Vietnam Primate Conservation Program.

The ‘Community based Protection Unit’ (CPU) comprising 30 locals from the 8 surrounding communes in the area, support the protection of the area and act as mediators for awareness raising in these communes. The work of the CPU is managed by the Management Board of the nature reserve.

In December 2016 a one week training program for the staff of the CPU and the rangers of the nature reserve was carried out to implement the SMART-Patrol Program for the patrol work in the nature reserve (Fig. 12). GPS units and computer were provided. The training was carried out by two experienced biologists from the Vietnamese NGO "Green Viet", Danang. The SMART-Patrol Program enables the Management Board to get a detailed overview about impacts to the reserve and biological information, with focus on the Delacour's langurs activities as well.

Fig.12. A training course for the SMART-Patrol Program took place in Van Long Nature Reserve to improve the patrol activities. Photo: Bui Van Tuan.

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The reintroduction project for lorises in Cuc Phuong National Park and for Hatinh langurs in Ke Go Nature Reserve were generously supported from an anonymous donor.

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We also would like to thank the NGO "Green Viet" for the very close cooperation and the great support for the SMART training program and for the reintroduction of the Hatinh langurs. Our thank goe's especially to the biologists Bui Van Tuan, Hoang Quoc Huy and Tran Huu Vy. The work of the NGO was essential for the implementation of the project. Many thanks also to the Management Board of Ke Go Nature Reserve and all the supporting rangers.

Publications and presentations resulting from the work of the Endangered Primate Rescue Center in 2015 and 2016

Hartmann C, **Göttling J**, **Nadler T** & **Streicher U** (2015): Effect of orally applied ivermectin on gastrointestinal nematodes in douc langurs (*Pygathrix* ssp.). Vietnamese J. Primatol. 2(3), 39-44.

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INSTRUCTIONS FOR CONTRIBUTORS

The **Vietnamese Journal of Primatology** is a peer reviewed journal. It welcomes manuscripts from all areas related to the conservation and research of non-human primate taxa which occur in Vietnam and the neighboring countries of Cambodia, China and Laos. The journal publishes both original research papers and review articles. Original papers may be published as standard research articles or as short communications.

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Papers published in periodicals

Dao Van Tien (1989): On the trends of the evolutionary radiation on the Tonkin Leaf monkey (*Presbytis francoisi*) (Primates: Cercopithecidae). J. of Human Evolution 4, 501-507.

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

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