State of the Apes

Infrastructure Development and Ape Conservation

Infrastructure development in Africa and Asia is expanding at breakneck speed, largely in biodiversity-rich developing nations. The trend reflects governments' efforts to promote economic growth in response to increasing populations, rising consumption rates and persistent inequalities. Large-scale infrastructure development is regularly touted as a way to meet the growing demand for energy, transport and food—and as a key to poverty alleviation. In practice, however, road networks, hydropower dams and "development corridors" tend to have adverse effects on local populations, natural habitats and biodiversity. Such projects typically weaken the capacity of ecosystems to maintain ecological functions on which wildlife and human communities depend, particularly in the face of climate change.

This volume—*State of the Apes: Infrastructure Development and Ape Conservation*—presents original research and analysis, topical case studies and emerging tools and methods to inform debate, practice and policy with the aim of preventing and mitigating the harmful impacts of infrastructure projects on biodiversity. Using apes as a proxy for wildlife and ecosystems themselves, it identifies opportunities for reconciling economic and social development with environmental stewardship.

This title is available as an open access eBook via Cambridge Core and at www.stateofapes.com.

State of the Apes

Series editors

Helga Rainer Arcus Foundation

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The world's primates are among the most endangered of all tropical species. All great ape species – gorilla, chimpanzee, bonobo and orangutan – are classified as either Endangered or Critically Endangered. Furthermore, nearly all gibbon species are threatened with extinction. Whilst linkages between ape conservation and economic development, ethics and wider environmental processes have been acknowledged, more needs to be done to integrate biodiversity conservation within broader economic, social and environmental communities if those connections are to be fully realized and addressed.

Intended for a broad range of policymakers, industry experts and decision-makers, academics, researchers and NGOs, the *State of the Apes* series will look at the threats to these animals and their habitats within the broader context of economic and community development. Each publication presents a different theme, providing an overview of how these factors interrelate and affect the current and future status of apes, with robust statistics, welfare indicators, official and various other reports providing an objective and rigorous analysis of relevant issues.

Other Titles in this Series

Arcus Foundation. 2015. *State of the Apes: Industrial Agriculture and Ape Conservation*. Cambridge: Cambridge University Press.

Arcus Foundation. 2014. *State of the Apes: Extractive Industries and Ape Conservation.* Cambridge: Cambridge University Press.

Other Language Editions

Bahasa Indonesia

Arcus Foundation. 2018. *Negara Kera: Pembangunan Infrastruktur dan Konservasi Kera.*

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State of the Apes

Infrastructure Development and Ape Conservation

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Foreword

Our world is on the verge of unprecedented economic and environmental change. While access to technology and opportunity are dramatically improving many parts of the planet, we also see climate change and widening inequality putting that progress in jeopardy. Even though new infrastructure investments—in roads, dams, pipelines and railways—promise economic prosperity for poorer countries, the risks such projects pose threaten to outweigh the benefits.

Look no further than what is happening to the world's population of apes across Africa and southeast Asia. The fragmentation and exploitation of tropical forests is a direct threat to apes—compromising their habitat, making food scarce, and bringing dangers like poaching and disease. As a result, their numbers are decreasing everywhere. Today, many ape species are on the precipice of extinction.

As this latest volume of *State of the Apes* argues, our well-being is inextricably linked to the well-being of our environment—and the well-being of all species that call our planet home.

That is in part because this same forest destruction is equally devastating to forest-dependent *people*. Industrial-scale infrastructure development has a significant, detrimental impact on local communities that have a long-term relationship with the forest. These rural and indigenous communities frequently don't see the economic benefits brought by new roads and power plants; instead they see their land taken away, without any just compensation or respect for their voices or rights.

Moreover, these developments have even wider ramifications for our environment. When we eliminate forests and fail to lift up the communities that protect them, we dramatically increase the amount of CO_2 in our atmosphere. When we abuse our lands, we severely weaken our position in the fight against climate change.

In other words, when apes are displaced—when their forests are degraded and their lives are devalued—humans are too. When we ignore the larger consequences of these massive infrastructure projects, especially in the name of inequitable and unjust gain, the whole world suffers.

Our planet and our communities are in urgent need of a more sustainable, equitable kind of economic development—one that empowers everyone, while protecting the planet's life and resources.

At the Ford Foundation, we understand that all these issues are deeply intertwined, and to address them comprehensively, the solutions must be similarly interconnected. The question is: how do we strike a balance that enables development while also allowing apes and other species, local communities, the environment and the economy to thrive?

This book is aimed at helping us answer that difficult question. Through reasoned, peer-reviewed science and practical examples, *State of the Apes* shows that though there may always be trade-offs, smart policy comes from considering what will create long-term benefits for all. It offers real solutions for how we plan, organize and educate to produce socially inclusive and green infrastructure. And it reminds us that both long-term environmental sustainability and long-term economic progress are the result of *equitable* and just solutions—not unsustainable or corrupt investments.

Most importantly, this volume demonstrates how equitable development is not only a possibility, but a necessity.

We know we can't stop the world from developing, but we can make sure inevitable and necessary developments in infrastructure also contribute to the larger march of progress for all people, and protect the

environment. It's up to all of us to ensure that these projects are executed thoughtfully, responsibly and sustainably—that they are not destructive, but truly constructive.

At this critical moment—when governments, businesses and civil society organizations across the world are coming up against the dual threats of climate change and economic inequality—it has never been more essential that we keep our shared future in mind.

The *State of the Apes* series makes clear that charting a path forward is not about the state, or fate, of any one species, but about the fair and sustainable solutions that our world so desperately needs.

Darren Walker
President
Ford Foundation

Contents

The Arcus Foundation

The Arcus Foundation is a private grant-making foundation that advances social justice and conservation goals. The Foundation works globally and has offices in New York City, USA and Cambridge, UK. For more information visit:

- arcusfoundation.org.

Or connect with Arcus at:

- twitter.com/ArcusGreatApes; and
- facebook.com/ArcusGreatApes.

Great Apes Program

The long-term survival of humans and the great apes is dependent on how we respect and care for other animals and our shared natural resources. The Arcus Foundation seeks to increase respect for and recognition of the rights and value of the great apes and gibbons, and to strengthen protection from threats to their habitats. The Arcus Great Apes Program supports conservation and policy advocacy efforts that promote the survival of great apes and gibbons in the wild and in sanctuaries that offer high-quality care, safety and freedom from invasive research and exploitation.

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Notes to Readers

Acronyms and abbreviations

A list of acronyms and abbreviations can be found at the back of the book, starting on p. 279.

Annexes

All annexes can be found at the back of the book, starting on p. 264, except for the Abundance Annex, which is available from the *State of the Apes* website:

- www.stateoftheapes.com.

Glossary

There is a glossary of scientific terms and keywords at the back of the book, starting on p. 282.

Chapter cross-referencing

Chapter cross-references appear throughout the book, either as direct references in the body text or in brackets.

Ape Range Maps

The ape range maps throughout this edition show the extent of occurrence (EOO) of each species. An EOO includes all known populations of a species contained within the shortest possible continuous imaginary boundary. It is important to note that some areas within these boundaries are unsuitable and unoccupied.

The Arcus Foundation commissioned the ape distribution maps in the Apes Overview, Figures AO1 and AO2, to provide the most accurate and up-to-date illustration of range data. These maps were created by the Max Planck Institute for Evolutionary Anthropology, who manage the A.P.E.S. portal and database. This volume also features maps created by contributors who used ape range data from other sources. As a consequence, the maps may not all align exactly.

Photographs

We aim to include photographs that are relevant to each theme and illustrate the content of each chapter. If you have photographs that you are willing to share with the Arcus Foundation, for use in this series, or for multiple purposes, please contact the Production Coordinator (awhite@arcusfoundation.org) or the Cambridge office.

Acknowledgments

The aim of the *State of the Apes* series is to facilitate critical engagement on conservation, industry and government practice and to expand support for great apes and gibbons. We are grateful to everyone who played a part, including meeting participants, our authors, contributors and reviewers, and those involved in the production of the book.

The support of Jon Stryker and the Arcus Foundation Board of Directors is essential to the production of this publication. We thank them for their ongoing support.

A key element outside of the thematic content is the overview of the status of apes, both in their natural habitats and in captivity. We extend our thanks to the captive-ape organizations that provided detailed information and to all the great ape and gibbon scientists who contribute their valuable data to build the A.P.E.S. database. Such collaborative efforts are key to effective and efficient conservation action.

Authors, contributors, reviewers and those who provided essential data and support are acknowledged at the end of each chapter. We could not have produced this book without them, and we thank them for their enduring patience and participation, in sickness and in health. Many of the photographs included were generously shared by their creators, who are credited alongside each one. Respect and thanks to those who read and reviewed the whole publication—no small task: Mihai Coroi, Cindy Rizzo and Tommaso Savini.

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We are committed to ensuring that these books are available to as many stakeholders as possible, not least by providing them in English, French and Bahasa Indonesia. Our thanks go to our cartographer, copy editor, graphic designers, indexer, proofreaders, reference editor and translators: Sarah Binns, Eva Fairnell, Tania Inowlocki, Caroline Jones, Rick Jones, Hyacinthe Kemp, Jillian Luff, Anton Nurcahyo, Islaminur Pempasa, Hélène Piantone, Erica Taube, Beth Varley and Rumanti Wasturini. All language editions are provided on the *State of the Apes* website, and our thanks go to the Arcus Communications team for managing this site, especially Stephanie Myers, Sebastian Naidoo and Bryan Simmons.

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Helga Rainer, Alison White and Annette Lanjouw
Editors

Apes Overview

APES INDEX

Bonobo (*Pan paniscus*)

Distribution and Numbers in the Wild

The bonobo is only present in the Democratic Republic of Congo (DRC), biogeographically separated from chimpanzees and gorillas by the Congo River (see Figure AO1). The population size is unknown, as only 30% of the species' historic range has been surveyed; however, estimates from the four geographically distinct bonobo strongholds suggest a minimum population of 15,000–20,000 individuals, with numbers decreasing (Fruth *et al*., 2016).

The bonobo is included in the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) Appendix I and is categorized as endangered on the International Union for Conservation of Nature (IUCN) Red List (Fruth *et al*., 2016; see Box AO1). The causes of population decline include poaching; habitat loss and degradation; disease; and people's lack of awareness that hunting and eating bonobos is unlawful. Poaching, which is mainly carried out as part of the commercial wild meat trade and for some medicinal purposes, has been exacerbated by the ongoing effects of armed conflict, such as military-sanctioned hunting and the accessibility of modern weaponry and ammunition (Fruth *et al*., 2016).

Physiology

Male adult bonobos reach a height of 73–83 cm and weigh 37–61 kg, while females are slightly smaller, weighing 27–38 kg. Bonobos are moderately sexually dimorphic and similar in size and appearance to chimpanzees, although with a smaller head and lither appearance. The maximum life span in the wild is 50 years (Hohmann *et al*., 2006; Robson and Wood, 2008).

The bonobo diet is mainly frugivorous (more than 50% fruit), supplemented with leaves, stems, shoots, pith, seeds, bark, flowers, honey and fungi, including truffles. Only a very small part of their diet consists of animal matter—such as insects, small reptiles, birds and medium-sized mammals, including other primates.

Social Organization

Bonobos live in fission–fusion communities of 10–120 individuals, consisting of multiple males and females. When foraging, they split into smaller mixed-sex subgroups, or parties, averaging 5–23 individuals.

Male bonobos cooperate with and tolerate one another; however, lasting bonds between adult males are rare, in contrast to the bonds between adult females, which are strong and potentially last for years. A distinguishing feature of female bonobos is that they are co-dominant with males and form alliances against certain males within the community. Among bonobos, the bonds between mother and son are the strongest, prove highly important for the social status of the son and last into adulthood.

Together with chimpanzees, bonobos are the closest living relatives to humans, sharing 98.8% of our DNA (Smithsonian Institution, n.d.; Varki and Altheide, 2005).

Chimpanzee (*Pan troglodytes*)

Distribution and Numbers in the Wild

Chimpanzees are widely distributed across equatorial Africa, with discontinuous populations from southern Senegal to western Uganda and Tanzania (Humle *et al*., 2016b; see Figure AO1).

Chimpanzees are listed in CITES Appendix I, and all four subspecies are categorized as endangered on the IUCN Red List. There are approximately 140,000 central chimpanzees (*Pan troglodytes troglodytes*); 18,000–65,000 western chimpanzees (*Pan t. verus*); 181,000–256,000 eastern chimpanzees (*Pan t. schweinfurthii*); and probably fewer than 6,000–9,000 Nigeria–Cameroon chimpanzees (*Pan t. ellioti*). Populations are believed to be declining, but the rate has not yet been quantified (Humle *et al*., 2016b).

Decreases in chimpanzee numbers are mainly attributed to increased poaching for the commercial wild meat trade, habitat loss and degradation, and disease (particularly Ebola) (Humle *et al*., 2016b).

Physiology

Male chimpanzees are 77–96 cm tall and weigh 28–70 kg, while females measure 70–91 cm and weigh 20–50 kg. They share many facial expressions with humans, although forehead musculature is less pronounced and they have more flexible lips. Chimpanzees live for up to 50 years in the wild.

Chimpanzees are mainly frugivorous and opportunistic feeders. Some communities include 200 species of food items in a diet of fruit supplemented by herbaceous vegetation and animal prey, such as ants and termites, but also small mammals, including other primates. Chimpanzees are the most carnivorous of all the apes.

Social Organization

Chimpanzees show fission–fusion, multi-male–multi-female grouping patterns. A large community includes all individuals who regularly associate with one another; such communities comprise an average of 35 individuals, with the largest-known group counting 150, although this size is rare. The community separates into smaller, temporary subgroups, or parties. The parties can be highly fluid, with members moving in and out quickly or a few individuals staying together for a few days before rejoining the community.

Typically, home ranges are defended by highly territorial males, who may attack or even kill neighboring chimpanzees. Male chimpanzees are dominant over female chimpanzees and are generally the more social sex, sharing food and grooming each other more frequently. Chimpanzees are noted for their sophisticated forms of cooperation, such as in hunting and territorial defense; the level of cooperation involved in social hunting activities varies across communities, however.

Gorilla (*Gorilla* species (spp.))

Distribution and Numbers in the Wild

The western gorilla (*Gorilla gorilla*) is distributed throughout western equatorial Africa and has two subspecies: the western lowland gorilla (*Gorilla g. gorilla*) and the Cross River gorilla (*Gorilla g. diehli*). The eastern gorilla (*Gorilla beringei*) is found in the DRC and across the border in Uganda and Rwanda. There are two subspecies of the eastern gorilla: the mountain gorilla (*Gorilla b. beringei*) and Grauer's gorilla (*Gorilla b. graueri*), also referred to as the eastern lowland gorilla (see Figure AO1).

All gorillas are listed as critically endangered on the IUCN Red List. Population estimates for the western gorilla range from 150,000 to 250,000, while as few as 250–300 Cross River gorillas remain in the wild (Bergl, 2006; Oates *et al*., 2007; Sop *et al*., 2015; Williamson *et al*., 2013). The most recent population estimate for Grauer's gorilla is 3,800, which indicates a 77% loss since 1994 (Plumptre, Robbins and Williamson, 2016c). Mountain gorillas are estimated to number at least 880 individuals (Gray *et al*., 2013; Roy *et al*., 2014). The main threats to both species are poaching for the commercial wild meat trade, habitat destruction and degradation, and disease (for the western gorilla, the Ebola virus in particular). The eastern gorilla is also threatened by civil unrest (Maisels, Bergl and Williamson, 2016a; Plumptre *et al*., 2016c).

Physiology

The adult male of the eastern gorilla is slightly larger (159–196 cm, 120–209 kg) than the western gorilla (138–180 cm, 145–191 kg). Both species are highly sexually dimorphic, with females being about half the size of males. Their life span ranges from 30 to 40 years in the wild. Mature males are known as "silverbacks" due to the development of a gray saddle with maturity.

The gorillas' diet consists predominantly of ripe fruit and terrestrial, herbaceous vegetation. More herbaceous vegetation is ingested while fruit is scarce, in line with seasonality and fruit availability, and protein gain comes from leaves and bark of trees; gorillas do not eat meat but occasionally consume ants and termites. Mountain gorillas have less fruit in their environment than lowland gorillas, so they feed mainly on leaves, pith, stems, bark and, occasionally, ants.

Social Organization

Western gorillas live in stable groups with multiple females and one adult male (silverback); in contrast, eastern gorillas are polygynous and can be polygynandrous, with groups that comprise one or more silverbacks, multiple females, their offspring and immature relatives. The average group consists of ten individuals, but eastern gorillas can live in groups of up to 65 individuals, whereas the maximum group size for the western gorilla is 22. Gorillas are not territorial and home ranges overlap extensively. Chest beats and vocalizations typically are used when neighboring silverbacks come into contact, but intergroup encounters may escalate into physical fights. Mutual avoidance is normally the adopted strategy for groups that live in the same areas.

Orangutan (*Pongo* spp.)

Distribution and Numbers in the Wild

The orangutan range is now limited to the forests of Sumatra and Borneo, but these great apes were once present throughout much of southern Asia (Wich *et al*., 2008, 2012a; see Figure AO2). Survey data indicate that in 2015 fewer than 15,000[1] Sumatran orangutans (*Pongo abelii*) and just under 105,000[2] Bornean orangutans (*Pongo pygmaeus* spp.) remained in the wild (Ancrenaz *et al*., 2016; Wich *et al*., 2016). As a result of continuing habitat loss and hunting, both the Sumatran orangutan and the Bornean orangutan are classified as critically endangered (Ancrenaz *et al*., 2016; Singleton *et al*., 2016). Both species are listed in Appendix I of CITES.

In November 2017, a new species of orangutan was described in three forest fragments in Sumatra's Central, North and South Tapanuli districts, which are part of the Batang Toru Ecosystem (Nater *et al*., 2017).[3] The Tapanuli orangutan (*Pongo tapanuliensis*) has a total distribution of about 1,100 km² (110,000 ha) and a population size of fewer than 800 individuals (Wich *et al*., 2016).[4]

The main threats to all orangutan species are habitat loss and fragmentation, and killings due to human–ape conflict, hunting and the international pet trade (Ancrenaz *et al*., 2016; Gaveau *et al*., 2014; Singleton *et al*., 2016; Wich *et al*., 2008).*

Physiology

Adult males can reach a height of 94–99 cm and weigh 60–85 kg (flanged) or 30–65 kg (unflanged). Females are 64–84 cm tall and weigh 30–45 kg, meaning that orangutans are highly sexually dimorphic. In the wild, males on Sumatra have a life expectancy of 58 years and females 53 years. No accurate data exist for the Bornean orangutan.

Fully mature males develop a short beard and protruding cheek pads, termed "flanges." Some male orangutans experience "developmental arrest," maintaining a female-like size and appearance for many years past sexual maturity; they are known as "unflanged" males. Orangutans are the only great ape to exhibit male bimaturism.

The orangutan diet mainly consists of fruit, but they also eat leaves, shoots, seeds, bark, pith, flowers, eggs, soil and invertebrates (termites (*Isoptera*) and ants (*Formicidae*)). Carnivorous behavior has also been observed, but at a low frequency (preying on species such as slow lorises (*Nycticebus*)).

Social Organization

The mother–offspring unit is the only permanent social unit among orangutans, yet social groupings between independent individuals do occur, although their frequency varies across populations (Wich, de Vries and Ancrenaz, 2009a). While females are usually relatively tolerant of each other, flanged males are intolerant of other flanged and unflanged males (Wich *et al*., 2009a). Orangutans on Sumatra are generally more social than those on Borneo and live in overlapping home ranges, with flanged males emitting "long calls" to alert others to their location (Delgado and Van Schaik, 2000; Wich *et al*., 2009a). Orangutans are characterized by an extremely slow life history, with the longest interbirth interval (6–9 years) of any primate species (Wich *et al*., 2004, 2009a).

Gibbons (*Hoolock* spp.; *Hylobates* spp.; *Nomascus* spp.; *Symphalangus* spp.)

All four genera of gibbon generally share ecological and behavioral attributes, such as social monogamy in territorial groups; vocalization through elaborate song (including complex duets); frugivory and brachiation (moving through the canopy using only the arms). Gibbons primarily consume fruit but have a varied diet including insects, flowers, leaves and seeds. Female gibbons have a single offspring every 2.5–3 years (S. Cheyne, personal communication, 2017). Gibbons are diurnal and sing at sunrise and sunset; they dedicate a significant part of the day to finding fruit trees within their territories.

Hoolock genus

Distribution and Numbers in the Wild

Three species comprise the *Hoolock* genus: the western hoolock (*Hoolock hoolock*), the eastern hoolock (*Hoolock leuconedys*) and the newly discovered Gaoligong or Skywalker hoolock (*Hoolock tianxing*) (Fan *et al*., 2017). The Mishmi Hills hoolock (*Hoolock h. mishmiensis*), the most recently discovered subspecies of western hoolock, was officially named in 2013 (Choudhury, 2013).

The western hoolock's distribution spans Bangladesh, India and Myanmar. The eastern hoolock lives in China, India and Myanmar (see Figure AO2). To date, the Gaoligong hoolock has only been seen in eastern Myanmar and southwestern China (Fan *et al*., 2017).

With an estimated population of 2,500 individuals, the western hoolock is listed as endangered on the IUCN Red List. The eastern hoolock has a much larger population, numbering 293,200–370,000, and is listed as vulnerable on the IUCN Red List. Both species are listed in CITES Appendix I, with the main threats identified as habitat loss and fragmentation, and hunting for food, pets and medicinal purposes. The Gaoligong hoolock is likely to be categorized as endangered but has not yet been formally listed on the IUCN Red List (Fan *et al*., 2017).

Physiology

An individual hoolock can have a head and body length of 45–81 cm and weigh 6–9 kg, with males slightly heavier than females. Like most gibbons, the *Hoolock* genus is sexually dichromatic, with the pelage (coat) of females and males differing in terms of patterning and color. Pelage also differs across species: unlike the western hoolock, the eastern one features a complete separation between the white brow markings and a white preputial tuft.

The diet of the western hoolock is primarily frugivorous, supplemented with vegetative matter such as leaves, shoots, seeds, moss and flowers. While little is known about the diet of the eastern hoolock, it most likely resembles that of the western hoolock.

Social Organization

Hoolocks live in family groups of 2–6 individuals, consisting of a mated adult pair and their offspring. They are presumably territorial, although no specific data exist. Hoolock pairs vocalize a "double solo" rather than the more common "duet" of various gibbons.

***Hylobates* genus**

Distribution and Numbers in the Wild

Nine species are currently included in the *Hylobates* genus, although there remains some dispute about whether Abbott's gray gibbon (*Hylobates abbottii*), the Bornean gray gibbon (*Hylobates funereus*) and Müller's gibbon (*Hylobates muelleri*) represent full species (see Table AO1).

This genus of gibbon occurs discontinuously in tropical and subtropical forests from southwestern China, through Indochina, Thailand and the Malay Peninsula to the islands of Sumatra, Borneo and Java (Wilson and Reeder, 2005; see Figure AO2). The overall estimated minimum population for the *Hylobates* genus is about 360,000–400,000, with the least abundant species being the moloch gibbon (*Hylobates moloch*) and most abundant being, collectively, the "gray gibbons" (Abbott's, the Bornean and Müller's gibbons), although no accurate population numbers are available for Abbott's gray gibbon.

All *Hylobates* species are listed as endangered on the IUCN Red List and are in CITES Appendix I. Three hybrid zones occur naturally and continue to coexist with the unhybridized species in the wild. The main collective threats facing the genus are deforestation, hunting and the illegal pet trade (S. Cheyne, personal communication, 2017; Mittermeier *et al*., 2013).

Physiology

Average height for both sexes of all species is approximately 46 cm and their weight ranges between 5 kg and 7 kg. With the exception of the pileated gibbon (*Hylobates pileatus*), species in the genus are not sexually dichromatic, although the lar gibbon (*Hylobates lar*) has two color phases, which are not related to sex or age.

Gibbons are mainly frugivorous. Figs are an especially important part of their diet and are supplemented by leaves, buds, flowers, shoots, vines and insects, while small animals and bird eggs form the protein input.

Social Organization

Hylobates gibbons are largely socially monogamous, forming family units of two adults and their offspring; however, polyandrous and polygynous units have been observed, especially in hybrid zones. Territorial disputes are predominantly led by males, who become aggressive towards other males, whereas females tend to lead daily movements and ward off other females.

***Nomascus* genus**

Distribution and Numbers in the Wild

Seven species make up the *Nomascus* genus (see Table AO1).

The *Nomascus* genus, which is somewhat less widely distributed than the *Hylobates* genus, is present in Cambodia, Laos, Vietnam and southern China (including Hainan Island; see Figure AO2). Population estimates exist for some

taxa: there are approximately 1,500 western black crested gibbons (*Nomascus concolor*), 130 Cao Vit gibbons (*Nomascus nasutus*) and 23 Hainan gibbons (*Nomascus hainanus*). Population estimates for the white-cheeked gibbons (*N. leucogenys* and *N. siki*) are not available except for some sites, yet overall numbers are known to be severely depleted. The yellow-cheeked gibbons (*N. annamensis* and *N. gabriellae*) have the largest populations among the *Nomascus* gibbons.

All species are listed in CITES Appendix I; in the IUCN Red List, four are categorized as critically endangered (*N. concolor*, *nasutus*, *hainanus* and *leucogenys*) and two as endangered (*N. siki* and *N. gabriellae*), while one—the northern yellow-cheeked crested gibbon (*Nomascus annamensis*)—is yet to be assessed (IUCN, 2017). Major threats to these populations include hunting for food, pets and for medicinal purposes, as well as habitat loss and fragmentation.

Physiology

Average head and body length across all species of this genus, for both sexes, is approximately 47 cm; individuals weigh around 7 kg. All *Nomascus* species have sexually dimorphic pelage; adult males are predominantly black while females are a buffy yellow. Their diet is much the same as that of the *Hylobates* genus: mainly frugivorous, supplemented with leaves and flowers.

Social Organization

Gibbons of the *Nomascus* genus are mainly socially monogamous; however, most species have also been observed in polyandrous and polygynous groups. More northerly species appear to engage in polygyny to a greater degree than southern taxa. Copulations outside monogamous pairs have been recorded, although infrequently.

***Symphalangus* genus**

Distribution and Numbers in the Wild

Siamang (*Symphalangus syndactylus*) are found in several forest blocks across Indonesia, Malaysia and Thailand (see Figure AO2); the species faces severe threats to its habitat across its range. No accurate estimates exist for the total population size. The species is listed in CITES Appendix I and is classified as endangered on the IUCN Red List.

Physiology

The siamang's head and body length is 75–90 cm, and adult males weigh 10.5–12.7 kg, while adult females weigh 9.1–11.5 kg. The siamang is minimally sexually dimorphic, and the pelage is the same across sexes: black. The species has a large inflatable throat sac.

Siamang rely heavily on figs and somewhat less on leaves—a diet that allows them to be sympatric with *Hylobates* gibbons in some locations, since the latter focus more on fleshy fruits. The siamang diet also includes flowers and insects.

Social Organization

Males and females call territorially, using their large throat sacs, and males will give chase to neighboring males. One group's calls will inhibit other groups nearby, and they will consequently take turns to vocalize. The groups are usually based on monogamous pairings, although polyandrous groups have been observed. Males may also adopt the role of caregiver for infants.

Notes:

All information is drawn from the *Handbook of the Mammals of the World, Volume 3: Primates* (Mittermeier, Rylands and Wilson, 2013), unless otherwise cited.

* For the Bornean orangutan, additional threats include forest fires and people's lack of awareness that they are protected by law. For the Sumatran orangutan, the current most important threat is a land use plan issued by the government of Aceh in 2013. The plan does not recognize that the Leuser Ecosystem is a National Strategic Area, a legal status that prohibits cultivation, development and other activities that would degrade the ecosystem's environmental functions (Singleton *et al*., 2016).

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Ape Socioecology

This section presents an overview of the socioecology of the seven non-human apes: bonobos, chimpanzees, gibbons (including siamangs), eastern gorillas, western gorillas, and Bornean and Sumatran orangutans.[5]

Gorillas, whose range extends across ten central African countries, are the largest living primate species and the most terrestrial of all the apes. Chimpanzees are the most wide-ranging ape species in Africa, occurring in 21 countries (Humle *et al.*, 2016b). Orangutans are found in Asia—in both Indonesia and Malaysia—and are the only ape species to have two distinct male types. Gibbons are the most numerous of the apes, with 20 species across Asia (see Table AO2).

Great Ape Socioecology

Social organization differs considerably across the three great ape genera. Chimpanzees and bonobos form dynamic communities, fissioning into smaller parties or coming together (fusioning) according to food availability and the presence of reproductively active females (Wrangham, 1986). Chimpanzee communities average 35 members, with a known maximum of 150 members (Mitani, 2009). Bonobo communities are usually composed of between 30 and 80 individuals (Fruth, Williamson and Richardson, 2013).

Gorillas live in cohesive social groups. The median group size in eastern gorillas is ten, with groups consisting of one or more silverback males with several females and their offspring, although group sizes can be much larger. Western lowland gorillas differ from eastern gorillas, with groups frequently comprising more than 20 individuals and about 40% of groups having a multi-male structure. Their large body size and largely vegetation-based diet enable them to live in

BOX AO1

IUCN Red List Categories and Criteria, and CITES Appendices

The IUCN Species Survival Commission assesses the conservation status of each species and subspecies using IUCN Red List categories and criteria. As all great apes and gibbons are categorized as vulnerable, endangered or critically endangered, this box presents details on a selection of the criteria for these three categories (see Table AO1). Full details of the IUCN Red List categories and criteria (in English, French and Spanish) can be viewed and downloaded at:

http://www.iucnredlist.org/technical-documents/categories-and-criteria.

Detailed guidelines on their use are available at:

http://www.iucnredlist.org/documents/RedListGuidelines.pdf.

Appendices I, II and III to the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) are lists of species afforded different levels or types of protection from overexploitation.

All non-human apes are in Appendix I, which comprises species that are the most endangered among CITES-listed animals and plants. As they are threatened with extinction, CITES prohibits international trade in specimens of these species, except when the purpose of the import is not commercial, for instance for scientific research. In these exceptional cases, trade may take place, provided it is authorized by both an import permit and an export permit (or re-export certificate). Article VII of the Convention provides for a number of exemptions to this general prohibition. For more information, see:

https://www.cites.org/eng/disc/text.php#VII.

Table AO1

Criteria for Categorization as Vulnerable, Endangered and Critically Endangered

IUCN Red List category	Risk of extinction in the wild	Number of mature individuals in the wild	Rate of population decline over the past 10 years or 3 generations
Vulnerable	High	<10,000	>50%
Endangered	Very high	<2,500	>50%
Critically endangered	Extremely high	<250	>80%

Table AO2

Great Apes and Gibbons

GREAT APES		
***Pan* genus**		
Bonobo (a.k.a. pygmy chimpanzee)	*Pan paniscus*	■ Democratic Republic of Congo (DRC)
Central chimpanzee	*Pan troglodytes troglodytes*	■ Angola ■ Cameroon ■ Central African Republic ■ DRC ■ Equatorial Guinea ■ Gabon ■ Republic of Congo
Eastern chimpanzee	*Pan troglodytes schweinfurthii*	■ Burundi ■ Central African Republic ■ DRC ■ Rwanda ■ Sudan ■ Tanzania ■ Uganda
Nigeria–Cameroon chimpanzee	*Pan troglodytes ellioti*	■ Cameroon ■ Nigeria
Western chimpanzee	*Pan troglodytes verus*	■ Ghana ■ Guinea ■ Guinea-Bissau ■ Ivory Coast ■ Liberia ■ Mali ■ Senegal ■ Sierra Leone[6]
***Gorilla* genus**		
Cross River gorilla	*Gorilla gorilla diehli*	■ Cameroon ■ Nigeria
Grauer's gorilla (a.k.a. eastern lowland gorilla)	*Gorilla beringei graueri*	■ DRC
Mountain gorilla	*Gorilla beringei beringei*	■ DRC ■ Rwanda ■ Uganda
Western lowland gorilla	*Gorilla gorilla gorilla*	■ Angola ■ Cameroon ■ Central African Republic ■ Equatorial Guinea ■ Gabon ■ Republic of Congo
***Pongo* genus**		
Northeast Bornean orangutan	*Pongo pygmaeus morio*	■ Indonesia ■ Malaysia
Northwest Bornean orangutan	*Pongo pygmaeus pygmaeus*	■ Indonesia ■ Malaysia
Southwest Bornean orangutan	*Pongo pygmaeus wurmbii*	■ Indonesia
Sumatran orangutan	*Pongo abelii*	■ Indonesia
Tapanuli orangutan[7]	*Pongo tapanuliensis*	■ Indonesia
GIBBONS (excluding subspecies)		
***Hoolock* genus**		
Eastern hoolock	*Hoolock leuconedys*	■ China ■ India ■ Myanmar
Gaoligong hoolock (a.k.a. Skywalker hoolock)	*Hoolock tianxing*	■ China ■ Myanmar
Western hoolock	*Hoolock hoolock*	■ Bangladesh ■ India ■ Myanmar

Table AO2

Continued

***Hylobates* genus**		
Abbott's gray gibbon	*Hylobates abbotti*	■ Indonesia ■ Malaysia
Agile gibbon (a.k.a. dark-handed gibbon)	*Hylobates agilis*	■ Indonesia ■ Malaysia
Bornean gray gibbon (a.k.a. northern gray gibbon)	*Hylobates funereus*	■ Indonesia ■ Malaysia ■ Brunei
Bornean white-bearded gibbon (a.k.a. Bornean agile gibbon)	*Hylobates albibarbis*	■ Indonesia
Kloss's gibbon (a.k.a. Mentawai gibbon)	*Hylobates klossii*	■ Indonesia
Lar gibbon (a.k.a. white-handed gibbon)	*Hylobates lar*	■ China ■ Indonesia ■ Lao People's Democratic Republic (PDR) ■ Malaysia ■ Myanmar ■ Thailand
Moloch gibbon (a.k.a. Javan gibbon, silvery gibbon)	*Hylobates moloch*	■ Indonesia
Müller's gibbon (a.k.a. Müller's gray gibbon, southern gray gibbon)	*Hylobates muelleri*	■ Indonesia
Pileated gibbon (a.k.a. capped gibbon, crowned gibbon)	*Hylobates pileatus*	■ Cambodia ■ Lao PDR ■ Thailand
***Nomascus* genus**		
Cao Vit gibbon (a.k.a. eastern black crested gibbon)	*Nomascus nasutus*	■ China ■ Viet Nam
Hainan gibbon (a.k.a. Hainan black crested gibbon, Hainan black gibbon, Hainan crested gibbon)	*Nomascus hainanus*	■ China (Hainan Island)
Northern white-cheeked crested gibbon (a.k.a. northern white-cheeked gibbon, white-cheeked gibbon)	*Nomascus leucogenys*	■ Lao PDR ■ Viet Nam
Northern yellow-cheeked crested gibbon (a.k.a. northern buffed-cheeked gibbon)	*Nomascus annamensis*	■ Cambodia ■ Lao PDR ■ Viet Nam
Southern white-cheeked crested gibbon (a.k.a. southern white-cheeked gibbon)	*Nomascus siki*	■ Lao PDR ■ Viet Nam
Southern yellow-cheeked crested gibbon (a.k.a. red-cheeked gibbon, buff-cheeked gibbon, buffy-cheeked gibbon)	*Nomascus gabriellae*	■ Cambodia ■ Lao PDR ■ Viet Nam
Western black crested gibbon (a.k.a. black crested gibbon, black gibbon, concolor gibbon, Indochinese gibbon)	*Nomascus concolor*	■ China ■ Lao PeDR ■ Viet Nam
***Symphalangus* genus**		
Siamang	*Symphalangus syndactylus*	■ Indonesia ■ Malaysia ■ Thailand

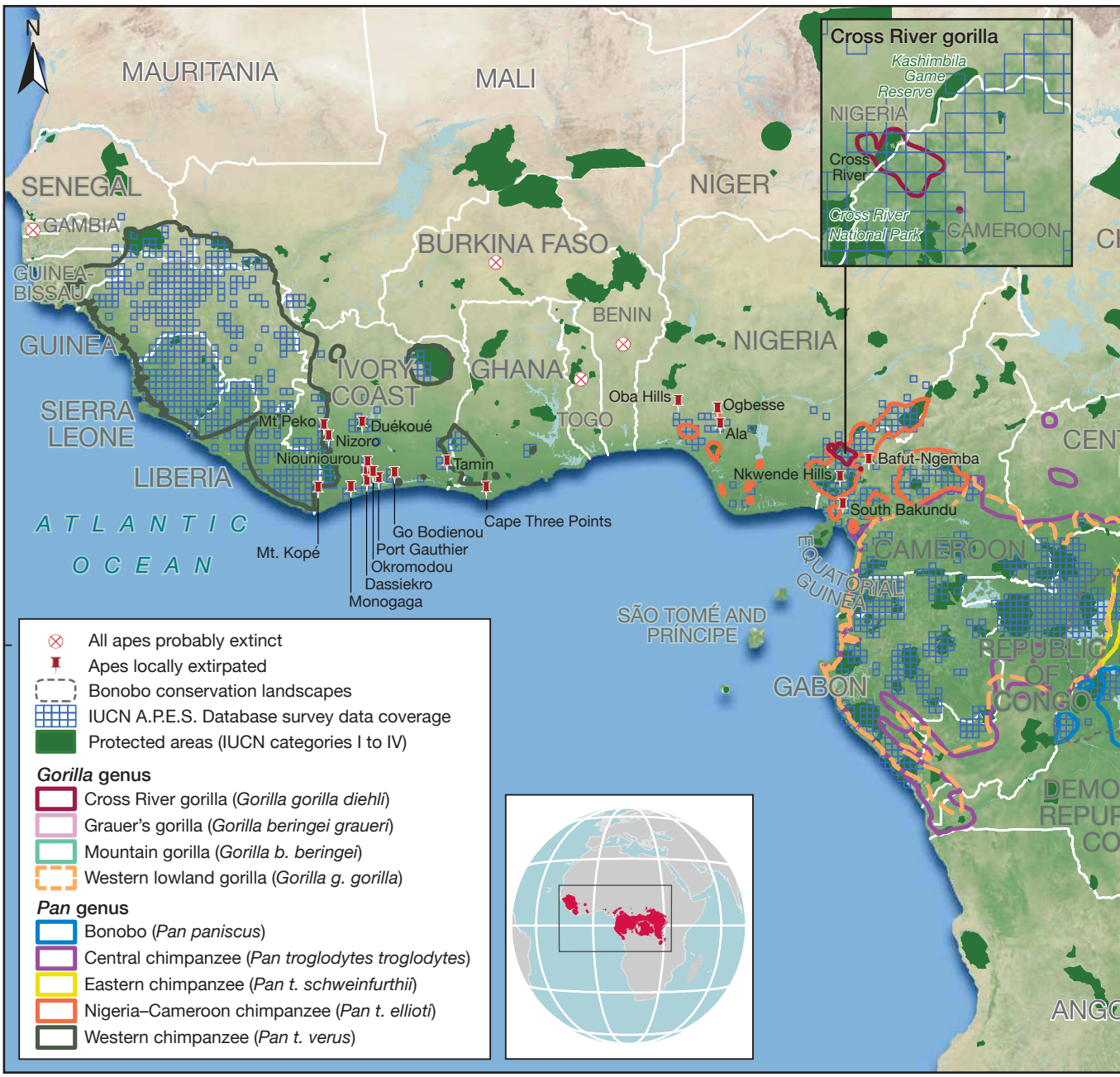
Sources: Susan Cheyne, personal communication, 2017; Elizabeth Macfie, personal communication, 2017; Mittermeier *et al*. (2013); Serge Wich, personal communication, 2017

environments with little fruit and to maintain stable groups, due to a lack of competition over highly nutritious foods.

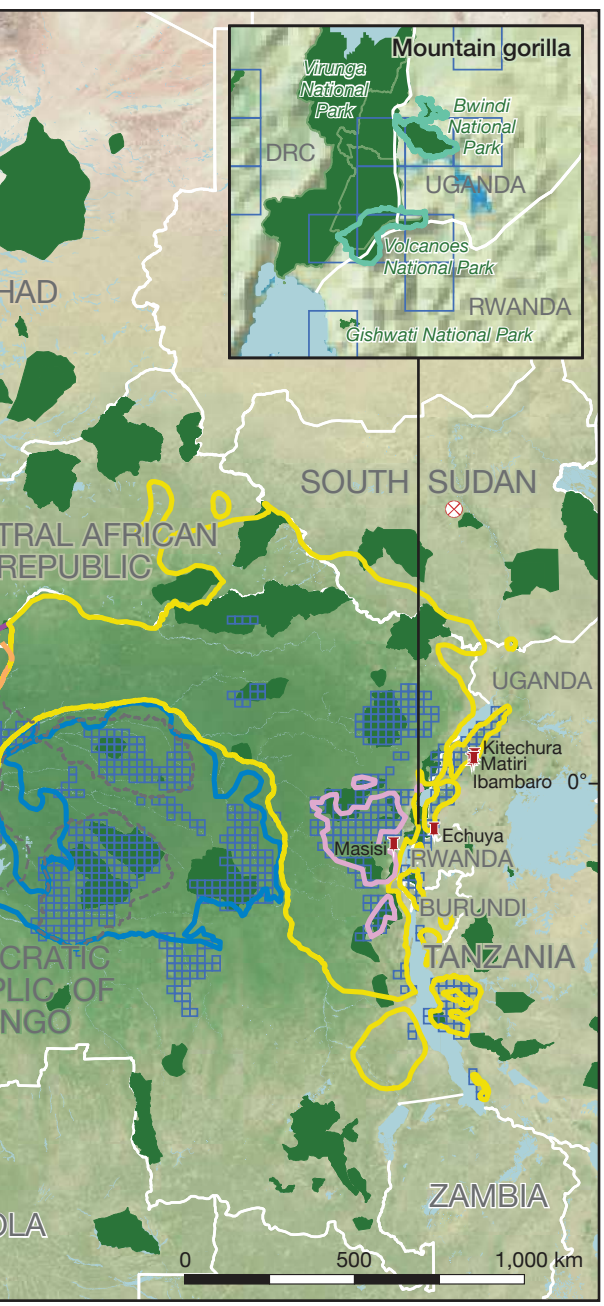
Orangutans have loosely defined communities. Flanged males, characterized by fatty cheek pads and large size, lead a semi-solitary existence (Emery Thompson, Zhou and Knott, 2012). Compared to flanged individuals, the smaller, unflanged adult males are more tolerant of other orangutans and,

Figure AO1

Ape Distribution in Africa[8]



like some adult females, they can travel together for a few hours and up to several days. Sumatran orangutans occasionally congregate when food is abundant (Wich *et al.*, 2006).



Habitat

Most great apes live in closed, moist, mixed tropical forest, occupying a range of various forest types, including lowland, swamp, seasonally inundated, gallery, coastal, submontane, montane and secondary regrowth. Some bonobo populations and eastern and western chimpanzees also live in savannah–woodland mosaic landscapes. The largest populations of great apes are found below 500 m elevation, in the lowland forests of Asia and Africa (Morrogh-Bernard *et al.*, 2003; Stokes *et al.*, 2010). Bonobos have a restricted, discontinuous range in the DRC, south of the Congo River (Fruth *et al.*, 2016). Eastern chimpanzees and eastern gorillas can range above 2,000 m altitude, and orangutans well above 1,000 m in both Sumatra and Borneo (Payne, 1988; Wich *et al.*, 2016).

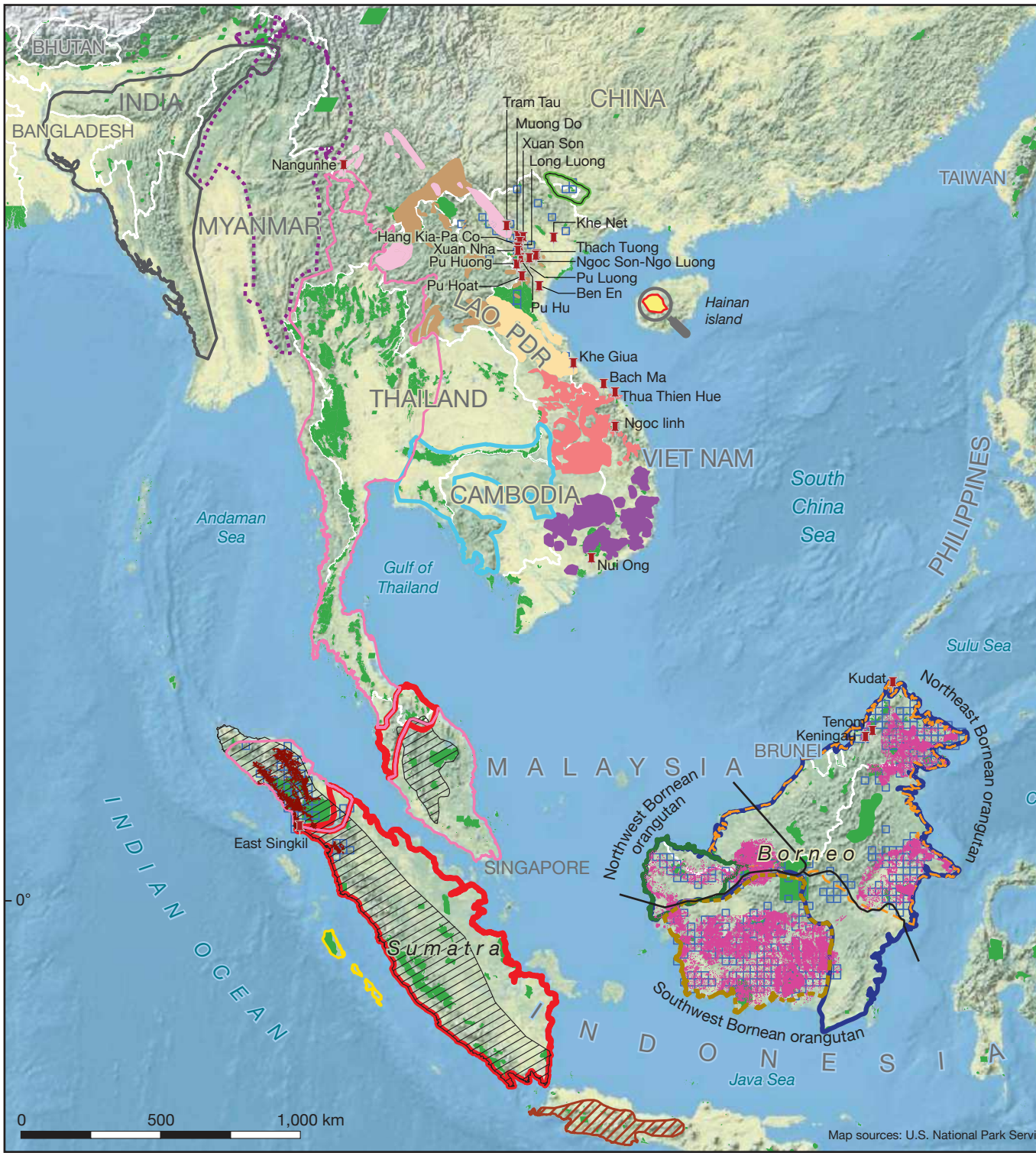
Most chimpanzees and bonobos inhabit evergreen forests, but some populations exist in deciduous woodland and drier savannah–woodland-dominated habitats interspersed with gallery forest. Although many populations inhabit protected areas, a great number of chimpanzee communities, especially on the western and eastern coasts of Africa, live outside of protected areas, including the majority of individuals in countries such as Guinea, Liberia and Sierra Leone (Brncic, Amarasekaran and McKenna, 2010; Kormos *et al.*, 2003; Tweh *et al.*, 2014). In Indonesian Borneo, more than half of the remaining orangutan populations are currently found outside of protected areas and large numbers of Sumatran orangutans also occur outside of protected areas (Wich *et al.*, 2011, 2012b).

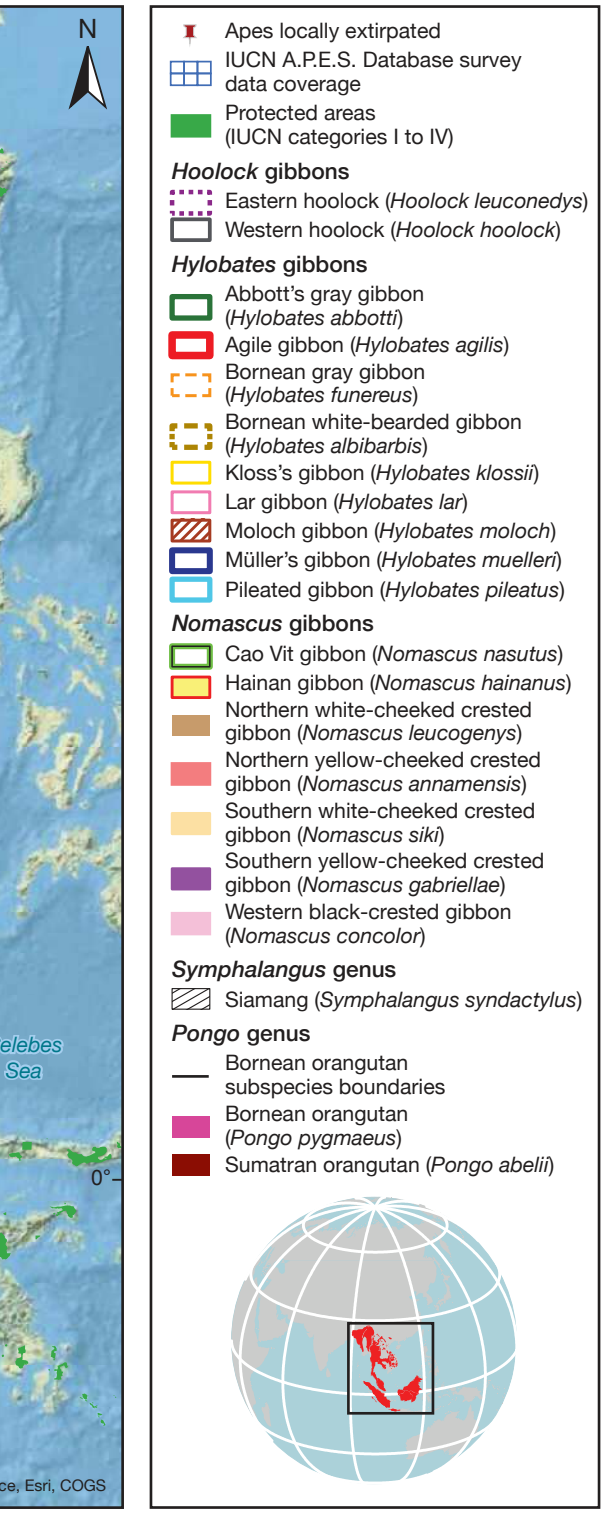
Daily Behaviour Patterns

Great apes are adapted to a plant diet, but all taxa consume insects, and some kill and eat small mammals. Succulent fruits are the main source of nutrition for bonobos, chimpanzees and orangutans, except at

Figure AO2

Ape Distribution in Asia[9]





altitudes where few fleshy fruits are available (Wright *et al.*, 2015). Gorillas rely heavily on herbaceous vegetation but consume a significant amount of fruit in nearly all locations (Robbins, 2011). During certain periods, African apes concentrate on terrestrial herbs or woody vegetation, such as bark. Similarly, in Asia, orangutans consume more bark and young leaves when fruits are scarce. Sumatran orangutans are more frugivorous than their Bornean relatives (Russon *et al.*, 2009).

The area used habitually by an individual, group or community of a species is referred to as a home range. Establishment of a home range helps secure access to resources within it (Delgado, 2010). Foraging in complex forest environments requires spatial memory and mental mapping. The great apes' daily searches for food are generally restricted to a particular location, an area of forest that a group or individual knows well. Chimpanzees are capable of memorizing the individual locations of thousands of trees over many years (Normand and Boesch, 2009); the other great ape species are likely to possess similar mental capacities.

Most great apes not only feed in trees, but also rest, socialize and sleep in them (although gorillas are largely terrestrial). Being large-brained, highly intelligent mammals, they need long periods of sleep. With the exception of gorillas, who nest primarily on the ground, great apes tend to spend the night in nests that they build high up in the trees, 10–30 m above ground (Morgan *et al.*, 2006). African apes are semi-terrestrial and often rest on the ground during the daytime, but orangutans are almost exclusively arboreal.

More or less restricted to the canopy, orangutans typically do not travel great distances. Bornean flanged adult males and adult females move 200 m each day, unflanged adult males usually double that distance. Sumatran orangutans move farther, but still less than 1 km each day on

average (Singleton *et al.*, 2009). The semi-terrestrial African apes range considerably longer distances and the most frugivorous roam several kilometers each day: bonobos and western lowland gorillas average 2 km, but sometimes 5–6 km, while chimpanzees travel 2–3 km, with occasional excursions up to 8 km. Savannah-dwelling chimpanzees generally range farther daily than their forest-dwelling counterparts.

Reproduction

Male apes reach sexual maturity between the ages of 8 and 18 years: chimpanzees attain adulthood at 8–15 years, bonobos at 10, eastern gorillas around 12–15 and western gorillas at 18. Orangutan males mature between the ages of 8 and 16 years, but they may not develop flanges for another 20 years (Wich *et al.*, 2004). Female great apes become reproductively active between the ages of 6 and 12 years: gorillas at 6–7 years, chimpanzees at 7–8, bonobos at 9–12 and orangutans at 10–11. They tend to give birth to their first offspring between the ages of 8 and 16: gorillas at 10 (with a range of 8–14 years), chimpanzees at 13.5 years (with a mean of 9.5–15.4 years at different sites), bonobos at 13–15 years and orangutans at 15–16 years.

Gestation periods in gorillas and orangutans are about the same as for humans; they are slightly shorter in chimpanzees and bonobos, at 7.5–8.0 months. Apes usually give birth to one infant at a time, although twin births do occur (Goossens *et al.*, 2011). Births are not seasonal; however, conception requires females to be in good health. Chimpanzees and bonobos are more likely to ovulate when fruit is abundant, so in some populations there are seasonal peaks in the numbers of conceiving females, with contingent peaks in the birth rate during particular months (Anderson, Nordheim and Boesch, 2006a; Emery Thompson and Wrangham, 2008). Bornean orangutans living in highly seasonal dipterocarp forests are most likely to conceive during mast fruiting events, when fatty seeds are plentiful (Knott, 2005). Sumatran orangutans do not face such severe constraints (Marshall *et al.*, 2009; Wich *et al.*, 2006). Meanwhile, gorillas show no seasonality in their reproduction, as they are less dependent on seasonal foods.

All great apes have slow reproductive rates, due to the mother's high investment in a single offspring and the infant's slow development and maturation. Infants sleep with their mother until they are weaned (4–5 years in African apes; 5–6 years in Bornean orangutans; 7 years in Sumatran orangutans) or a subsequent sibling is born. Weaning marks the end of infancy for African apes, but orangutan infants remain dependent on their mothers until they reach 7–9 years of age (van Noordwijk *et al.*, 2009). Females cannot become pregnant while an infant is nursing because suckling inhibits the reproductive cycle (Stewart, 1988; van Noordwijk *et al.*, 2013). Consequently, births are widely spaced, occurring on average every 4–7 years in African apes, every 6–8 years in Bornean orangutans and every 9 years in Sumatran orangutans. Interbirth intervals can be shortened by the death or killing of unweaned offspring. Infanticide, typically by an unrelated adult male, has been observed in gorillas (Harcourt and Greenberg, 2001; Watts, 1989). Infanticide has not been observed in orangutans or bonobos, but if a female chimpanzee with an infant transfers to a different group, her offspring is likely to be killed by a male in her new group, resulting in early resumption of her reproductive cycle (Wilson and Wrangham, 2003).

Long-term research on mountain gorillas and chimpanzees has allowed female lifetime reproductive success to be evaluated. The mean birth rate is 0.2–0.3 births per adult female per year, or one birth per adult female every 3.3–5.0 years. Mountain

gorilla females produce an average of 3.6 offspring during their lifetimes (Robbins *et al.*, 2011). Although female chimpanzees occasionally have twins, they usually give birth to a single surviving offspring approximately every 5 to 6 years. However, in their lifetime, female chimpanzees typically produce only 1 to 4 offspring who will survive to reproductive age (Thompson, 2013).

Key points to be noted are (1) that documenting the biology of long-lived species takes decades of research due to their slow rates of reproduction, and (2) that great ape populations that have declined in numbers are likely to take several generations to recover (generation time in the great apes is 20–25 years) (IUCN, 2014d). These factors make great apes far more vulnerable than smaller, faster-breeding species. Orangutans have the slowest life history of any mammal, with later age at first reproduction, longer interbirth intervals and longer generation times than African apes (Wich *et al.*, 2009a, 2009b); as a result, they are the most susceptible to loss.

Gorillas

Gorillas live in a broad range of habitats across Africa. As a result of their dietary patterns, they are restricted to moist forest habitats (at altitudes ranging from sea level to more than 3,000 m) and are not found in forest–savannah mosaics or gallery forests inhabited by chimpanzees and bonobos.

Across their range, gorillas rely more heavily than any other ape species on herbaceous vegetation, such as the leaves, stems and pith of understory vegetation, as well as leaves from shrubs and trees (Doran-Sheehy *et al.*, 2009; Ganas *et al.*, 2004; Masi, Cipolletta and Robbins, 2009; Wright *et al.*, 2015; Yamagiwa and Basabose, 2009). Early research suggested that gorillas ate very little fruit, a finding that can be attributed to the fact that initial studies of their dietary patterns were conducted in the Virunga Volcanoes, the only habitat in which gorillas eat almost no fruit as it is virtually unavailable (Watts, 1984). These conclusions were adjusted once detailed studies were conducted on gorillas living in lower-altitude habitats (Doran-Sheehy *et al.*, 2009; Masi *et al.*, 2015; Rogers *et al.*, 2004; Wright *et al.*, 2015; Yamagiwa *et al.*, 2003).

Gorillas incorporate a notable amount of fruit into their diets when it is available, but they are less frugivorous than bonobos and chimpanzees, preferring vegetative matter even at times of high fruit availability (Head *et al.*, 2011; Morgan and Sanz, 2006; Yamagiwa and Basabose, 2009). They rely heavily on terrestrial herbaceous vegetation, which often increases in availability in disturbed landscapes, such as abandoned farmland or plantations, selectively logged land, and areas that border on human settlements.

Mountain gorillas are primarily terrestrial. Although western gorillas are more arboreal, they still primarily travel on the ground and not through the tree canopy. The distance traveled per day by gorillas declines with increasing availability of understory vegetation, varying between approximately 500 m and 3 km per day (Robbins, 2011).

Eastern gorillas range over areas of 6–34 km² (600–3,400 ha) (Robbins, 2011; Williamson and Butynski, 2013a); western gorilla home ranges average 10–20 km² (1,000–2,000 ha), and potentially up to 50 km² (5,000 ha) (Head *et al.*, 2013). Gorillas are not territorial but have overlapping home ranges that they do not actively defend. However, there is evidence that they have non-overlapping, exclusive core areas (the zone used the most by a group), suggesting that groups do partition their habitat (Seiler *et al.*, 2017).

As the density of gorillas increases, the degree of home range overlap can increase dramatically, as can the frequency of intergroup encounters (Caillaud *et al.*, 2014);

results can include increased fighting, injuries and mortality. Encounters between groups can occur without visual contact, as silverbacks may exchange vocalizations and chestbeats until one or both groups move away. Some encounters between groups involve more than auditory contact, however, and can escalate to include aggressive displays or fights (Bradley *et al.*, 2004; Robbins and Sawyer, 2007). Physical aggression is rare, but if contests escalate, fighting between silverbacks can be intense. Some gorillas have died from infections of injuries sustained during such interactions (Williamson, 2014).

Chimpanzees and Bonobos

Chimpanzees eat mainly fruit, although they have an omnivorous diet, which may include plant pith, bark, flowers, leaves and seeds, as well as fungi, honey, insects and mammal species, depending on the habitat and the community; some groups may consume as many as 200 plant species (Humle, 2011). Terrestrial and arboreal, chimpanzees live in multi-male–multi-female, fission–fusion communities. A single community will change size by fissioning into smaller parties according to resource availability and activity (food and access to reproductive females). Parties thus tend to be smaller during periods of fruit scarcity. Adult female chimpanzees frequently spend time alone with their offspring or in a party with other females.

Chimpanzees have home ranges of 7–41 km² (700–4,100 ha) in forest habitats and more than 65 km² (6,500 ha) in savannah (Emery Thompson and Wrangham, 2013; Pruetz and Bertolani, 2009). Male chimpanzees are highly territorial and patrol the boundaries of their ranges. Parties of males may attack members of neighboring communities and some populations are known for their aggression (Williams *et al.*, 2008). After a fight, victors may seize females or territory from the vanquished.

Bonobo communities share home ranges of 20–60 km² (2,000–6,000 ha) (Fruth *et al.*, 2013). Bonobos exhibit neither territorial defense nor cooperative patrolling; encounters between members of different communities involve excitement rather than conflict (Hohmann *et al.*, 1999).

Chimpanzees and bonobos both live in multi-male and multi-female groups and are semi-terrestrial. The size of their home ranges varies in line with their group size, the quality of the habitat and food availability, which may change from season to season. Bonobos are not territorial, whereas chimpanzees are generally highly intolerant of neighboring groups; intergroup encounters can result in lethal aggressive attacks among males in particular. The frequency of such encounters can be exacerbated by shifts in home ranges linked to habitat loss, changes in habitat quality and disruptions in their environment (e.g. roads, logging) (Watts *et al.*, 2006; Wilson *et al.*, 2014b).

Bonobos are generally frugivorous but are more dependent on terrestrial herbaceous vegetation, including aquatic plants, than chimpanzees (Fruth *et al.*, 2016).

Wherever gorillas and chimpanzees are sympatric, dietary divisions between the species limit direct competition for food (Head *et al.*, 2011). If the area of available habitat is restricted, such mechanisms for limiting competition are compromised (Morgan and Sanz, 2006).

Orangutans

Male orangutans are the dispersing sex: upon reaching sexual maturity, they leave the area where they were born to establish their own range. A male orangutan's range encompasses several (smaller) female ranges. High-status flanged males are able to monopolize both food and females to a degree and

may thus temporarily reside in a relatively small area—typically 4–8 km² (400–800 ha) for Bornean males (Mittermeier *et al.*, 2013). Orangutan home range overlap is usually extensive, but flanged orangutans establish personal space by emitting long calls. As long as distance is maintained, physical conflicts are rare; however, close encounters between adult males trigger aggressive displays that sometimes lead to fights. If an orangutan inflicts serious injury on his opponent, infection of the wounds can result in death (Knott, 1998).

Although they are primarily fruit-eaters, orangutans are able to adapt their diet to what is available in the forest. In Borneo, they feed on more than 500 plant species (Russon *et al.*, 2009). The resilience of orangutans and their ability to cope, albeit temporarily, with drastic habitat changes is further illustrated by recent records of species presence in acacia plantations in East Kalimantan (Meijaard *et al.*, 2010a); a mosaic of mixed agriculture in Sumatra (Campbell-Smith *et al.*, 2011a); oil palm plantations in Borneo (Ancrenaz *et al.*, 2015b); and in forests exploited for timber (Ancrenaz *et al.*, 2010; Wich *et al.*, 2016).

It must be noted, however, that orangutan presence in these human-altered landscapes does not imply the species' long-term survival. Orangutan survival is still dependent on a landscape mosaic with adequate forest patches for food, shelter and other needs. Today, half of the wild orangutan populations in Indonesian Borneo are surviving outside of protected forests, in areas that are prone to human development and transformation (Wich *et al.*, 2012b).

Orangutans are the largest arboreal mammals in the world, but recent studies have shown that they also walk on the ground for considerable distances in all types of natural and man-made habitats (Ancrenaz *et al.*, 2014; Loken, Boer and Kasyanto, 2015; Loken, Spehar and Rayadin, 2013). Consequently, orangutans are able to cross open artificial infrastructures to a certain extent. In Sabah, Malaysian Borneo, for example, orangutans have been seen crossing sealed and dust roads when traffic is not too heavy. Greater terrestriality in orangutans will increase the risk of contracting diseases that the animals are not usually exposed to when they live in the tree canopy; however, there is a dearth of information about such new risks. When territories of resident individuals are destroyed, it is difficult for them to establish a new territory if other animals already reside in nearby areas. Indeed, resident animals who have lost their territory, and cannot easily establish a new range, slowly die off. However, adult unflanged males do not have a territory and can thus move away from a disturbed area and return after the source of nuisance has been eliminated (Ancrenaz *et al.*, 2010).

Gibbon Socioecology

Gibbons are the most diverse and widespread group of apes. Currently, 20 species of gibbon in 4 genera are recognized:

- 9 *Hylobates* species;
- 7 *Nomascus* species;
- 3 *Hoolock* species; and
- the single *Symphalangus* species (Fan *et al.*, 2017; IUCN, 2017).

Gibbons inhabit a wide range of habitats, predominantly lowland, submontane and montane broadleaf evergreen and semi-evergreen forests, as well as dipterocarp-dominated and mixed-deciduous (that is, non-evergreen) forests. Some members of the *Nomascus* genus also occur in limestone karst forests and some populations of *Hylobates* live in peat-swamp forest (Cheyne, 2010). Gibbons occur from sea level up to around 1,500–2,000 m above sea level,

although their distribution is taxon- and location-specific; *Nomascus concolor*, for example, has been recorded at up to 2,900 m above sea level in China (Fan, Jiang and Tian, 2009).

All gibbons are heavily impacted by the extent and quality of forest as they are arboreal. Only rarely do they move bipedally and terrestrially across forest gaps or to access isolated fruiting trees in more degraded and fragmented habitats (Bartlett, 2007).

Gibbons are reliant on forest ecosystems for food. Gibbon diets are characterized by high levels of fruit intake, dominated by figs and supplemented with young leaves, mature leaves and flowers (Bartlett, 2007; Cheyne, 2008; Elder, 2009). Siamangs are more folivorous than other gibbons (Palombit, 1997). Reliance on other protein sources, such as insects, birds' eggs and small vertebrates, is probably underrepresented in the literature. The composition of the diet changes with the seasons and habitat type, with flowers and young leaves dominating during the dry season in peat-swamp forests and figs dominating in dipterocarp forests (Cheyne, 2010; Fan and Jiang, 2008; Lappan, 2009; Marshall and Leighton, 2006). Since gibbons are important seed dispersers, their frugivorous nature is significant in maintaining forest diversity (McConkey, 2000, 2005; McConkey and Chivers, 2007).

Gibbons are highly territorial and live in semi-permanent family groups defending a core area to the exclusion of other gibbons. Their territories average 0.42 km² (42 ha) (Bartlett, 2007); however, there is considerable variation and some indication that the more northerly *Nomascus* taxa maintain larger territories, possibly related to lower resource abundance at some times of year in these more seasonal forests.

Gibbons have been typified as forming socially monogamous family groups. Some studies, however, reveal that they are not necessarily sexually monogamous (Palombit, 1994). Notable exceptions include extra-pair copulations (mating outside of the pair bond), individuals leaving the home territory to take up residence with neighboring individuals and male care of infants (Lappan, 2008; Palombit, 1994; Reichard, 1995). Research also indicates that the more northerly Cao Vit, Hainan and western black crested gibbons commonly form polygynous groups with more than one breeding female (Fan and Jiang, 2010; Fan *et al.*, 2010; Zhou *et al.*, 2008). There is no conclusive argument regarding these variable social and mating structures; they may be natural or a by-product of small population sizes, compression scenarios or suboptimal habitats.

Both males and females disperse from their natal groups and establish their own territories (Leighton, 1987); females have their first offspring at around 9 years of age. Data from captivity suggest that gibbons become sexually mature as early as 5.5 years of age (Geissmann, 1991). Interbirth intervals are in the range of 2–4 years, with 7 months gestation (Bartlett, 2001; Geissmann, 1991). Captive individuals have lived upwards of 40 years; gibbon longevity in the wild is unknown but thought to be considerably shorter. Due to gibbons' relatively late age of maturation and long interbirth intervals, their reproductive lifetime may be only 10–20 years (Palombit, 1992). Population replacement in gibbons is therefore relatively slow.

Group demography changes only in the event of a death of one of the adults, as there is no regular immigration or emigration into these social groups. Gibbons in habitat fragments are isolated from other groups and dispersal is compromised, which may cause long-term issues regarding the sustainability of these populations. There is insufficient information about dispersal distances for subadult gibbons to determine maximum distances over which they could disperse (perhaps with the assistance of canopy

bridges). Gibbons have not been observed to crop-raid—either from plantations or small-scale farms—but this lack of information does not mean gibbons will not exploit disturbed areas if necessary.

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Endnotes

1 This estimate for Sumatran orangutans is higher than that of about 6,500 individuals cited in the previous volume of *State of the Apes* because it considers three new factors: "a) orangutans were found in greater numbers at higher altitudes than previously supposed (i.e., up to 1,500 m asl [above sea level] not just to 1,000 m asl), b) they were found to be more widely distributed in selectively-logged forests than previously assumed, and c) orangutans were found in some previously unsurveyed forest patches. The new estimate does not, therefore, reflect a real increase in Sumatran orangutan numbers. On the contrary, it reflects only much improved survey techniques and coverage, and hence more accurate data. It is extremely important to note, therefore, that overall numbers continue to decline dramatically" (Singleton *et al.*, 2016).

2 This estimate for Bornean orangutans is higher than the figure cited in the previous volume of *State of the Apes*, which suggests that about 54,000 individuals inhabited 82,000 km² (8.2 million ha) of forest (Wich *et al.*, 2008). Modeling and the latest field data available for Borneo were used to revise the map of the current distribution of Bornean orangutans; the range now covers an estimated 155,000 km² (15.5 million ha), or 21% of Borneo's landmass (Gaveau *et al.*, 2014; Wich *et al.*, 2012b). As Ancrenaz *et al.* (2016) explain: "If the mean average orangutan density recorded in 2004 (0.67 individuals/km²) is applied to the updated geographic range, then the total population estimate would be 104,700 individuals. This represents a decline from an estimated 288,500 individuals in 1973 and is projected to decline further to 47,000 individuals by 2025. [. . .] many populations will be reduced or become extinct in the next 50 years (Abram *et al.*, 2015)."

3 The Tapanuli orangutan was described and distinguished from the Sumatran orangutan as this volume of *State of the Apes* was being finalized for publication. As a consequence, this new species is only mentioned in the Apes Index, Table AO2 of this Overview and Case Study 6.4, and not in the rest of the volume.

4 The distribution and population estimates for the Tapanuli orangutan are based on earlier surveys in the area where the species occurs. Since these individuals were still being identified as Sumatran orangutans at the time of the surveys, the cited reference does not mention the Tapanuli orangutan.

5 For more detailed information, refer to Emery Thompson and Wrangham (2013), Reinartz, Ingmanson and Vervaecke (2013), Robbins (2011), Wich *et al.* (2009b), Williamson and Butynski (2013a, 2013b), and Williamson *et al.* (2013).

6 Some of these countries were erroneously omitted in the previous volume of *State of the Apes*. Benin, Burkina Faso, Gambia and Togo have been removed from the list as *Pan troglodytes verus* are extinct/possibly extinct in these countries.

7 See Endnote 3.

8 The Arcus Foundation commissioned the ape distribution maps (Figures AO1 and AO2) for this publication, so as to provide the most accurate and up-to-date illustration of range data. This volume also features maps created by contributors who used ape range data from different sources. As a consequence, the maps may not all align exactly.

9 See Endnote 8.

Photo: Large dams affect the political, social and environmental landscape of a region. Bakun Hydroelectric Dam, Malaysia © MOHD RASFAN/AFP/Getty Images