State of the Apes 2015

Industrial Agriculture and Ape Conservation

Social and economic systems worldwide are changing rapidly. These changes are accompanied by an increasing global demand for natural resources, including land, water, minerals, energy sources, food and timber. Today's foremost challenge lies in finding the tools not only to address the complexity of these interrelated trends, but also to implement strategies to balance environmental needs with socioeconomic requirements. This volume of *State of the Apes* contributes to this search by presenting original research and analysis, topical case studies and emerging best practice from a range of key stakeholders to examine the interface between ape conservation and industrial agriculture. In assessing the drivers behind agricultural expansion and land investments, it sheds light on governance challenges and legal frameworks that shape land use.

Aimed at policy-makers, industry experts and decision-makers, academics, researchers and NGOs, this volume is designed to inform debate, practice and policy in ways that will help to reconcile the goals of industrial agriculture with those of ape conservation and welfare, and social and economic development.

State of the Apes

Series editors

Helga Rainer Arcus Foundation

Alison White

Annette Lanjouw Arcus Foundation

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 policy-makers, 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. 2014. *State of the Apes: Extractive Industries and Ape Conservation.* Cambridge: Cambridge University Press.

Foreign Language Editions

Arcus Foundation. 2014. *La Planète des Grands Singes: Les Industries Extractives et la Conservation des Grands Singes.* Cambridge, UK: Arcus Foundation. Available from: www.stateoftheapes.com

Arcus Foundation. 2014. *Negara Kera: Industri Ekstraktif dan Konservasi Kera.* Cambridge, UK: Arcus Foundation. Available from: www.stateoftheapes.com

State of the Apes 2015

Industrial Agriculture and Ape Conservation

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Foreword

Last year I visited the Indonesian part of Borneo. One of the highlights was a visit to an orangutan shelter on an island covered by rainforest. There I learned that an orangutan builds a new nest every day, using leaves and branches in the trees. These great apes move around from tree to tree and hardly ever come down to the ground. When it rains, they make "umbrellas" from big leaves. Orangutans share more than 96% of their genetic makeup with humans. In fact, the name orangutan means "person of the forest." Many orangutans have lost their habitat because of deforestation. They have become homeless and dependent upon shelters to survive.

It is widely recognized that humans are altering the natural world at an unprecedented rate. Among the greatest challenges facing us today are understanding how human social and economic systems drive these changes and implementing strategies for reconciling economic development with the protection and conservation of the very resources upon which it depends. Future generations will judge us by how we have changed our behavior to ensure that we can live within the limits imposed on us by climate, water and land. They will also evaluate our efforts to ensure social justice and respect for dignity and life, while safeguarding the beauty and diversity of nature.

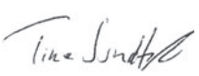
The *State of the Apes* series aims to identify and raise awareness of potential solutions for the conservation of biodiversity—and the environment more broadly—within the parameters of ongoing economic development. The tropical forests of Asia and Africa are the natural home of great apes and gibbons. By focusing on apes as flagship species for the conservation of these valuable forests, *State of the Apes* seeks to stimulate dialogue and collaboration, while also informing policy and practice.

Given that tropical forest loss is a significant contributor to climate change, the conservation of these resources is critical to protecting not only the great ape and gibbon populations but also the global human population. Even if tree crops replace the natural forest that has been removed, the impact on climate change will not be countered. And the loss of species diversity will be irreversible.

This volume highlights the deleterious effects of industrial-scale agriculture on ape populations as well as other wildlife species, forests and people in South and Southeast Asia to date. It warns that the shift from small-scale agriculture to industrial agriculture in Africa is likely to follow a similar path.

It also presents detailed case studies that show how governments, the private sector, local communities and civil society can work together to reconcile some of the conflicting agendas. In Liberia, for example, a recent agreement with the Government of Norway for results-based development aid holds significant promise for ensuring that decision-making on agricultural expansion takes biodiversity and land use planning into consideration, thereby protecting ape habitats, local communities and wildlife populations. And in Indonesia, major palm oil companies recently committed to establishing deforestation-free value chains.

Our survival depends on finding solutions that will help to preserve biodiversity while simultaneously securing human development and wellbeing. *State of the Apes* demonstrates that the conservation of flagship species—in this case, our closest relatives—can be achieved in conjunction with economic and social development, through integrated planning and sensitive policy and practice.



Tine Sundtoft
Minister of Climate and Environment,
Norway

NORWEGIAN MINISTRY OF CLIMATE AND ENVIRONMENT

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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 and to connect with Arcus visit:

- arcusfoundation.org.
- 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 page 264.

Annexes

All annexes can be found at the back of the book, starting on page 260, 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 key words at the back of the book, starting on page 268.

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.

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 this second volume of *State of the Apes* is to facilitate critical engagement on current conservation, industry and government practice and to expand support for great apes and gibbons. We are grateful to everyone who played a part, from meeting participants, to our authors, contributors and reviewers and those involved in the production and design 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 situ 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 named at the end of each chapter. We could not have produced this book without them. Most of the photographs included were generously shared by their creators, who are credited alongside each one. We are also grateful to the organizations that allowed us to include extracts from previously published articles, books and reports. Many others contributed by providing introductions, anonymous comments or strategic advice, helping with essential administrative tasks and providing much-appreciated moral support.

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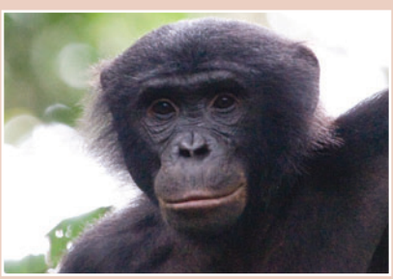
Each volume in this series is an extensive undertaking. We are committed to ensuring that these books are available to as many stakeholders as possible, not least by translating them into French, Bahasa Indonesia, and, beginning with this volume, Mandarin. We are delighted that GRASP has partnered with the Arcus Foundation in this endeavor, taking on the translations and the production of the translated editions, and we are thankful for their invaluable support.

Helga Rainer, Alison White and Annette Lanjouw
Editors

Apes Overview

APES INDEX



Bonobo (*Pan paniscus*)

Location and Population

The bonobo is only present in the Democratic Republic of Congo (DRC), biogeographically separated from chimpanzees and gorillas by the Congo River. The population size is unknown, as only 30% of its historic range has been surveyed; however, estimates place the population somewhere between 29,500 (Myers Thompson, 1997) and 50,000 (Dupain and Van Elsacker, 2001) individuals, with numbers decreasing. 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 (EN) on the International Union for Conservation of Nature (IUCN) Red List (Fruth *et al.*, 2008); for more information, see Box 2: IUCN Red List categories and criteria, and CITES Appendices. Activities causing population decline include poaching for the commercial wild meat trade, civil conflict and habitat destruction (Fruth *et al.*, 2008).

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.

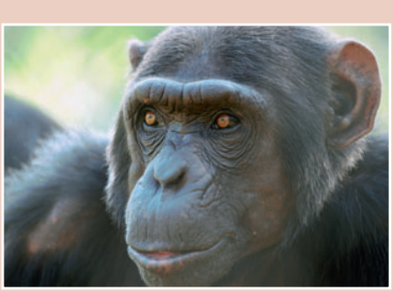
The bonobo diet is mainly frugivorous (more than 50% fruit), supplemented with leaves, stems, shoots, pith, seeds, bark, flowers, honey and fungi, including truffles. Animal matter—such as insects, small reptiles, birds and medium-sized mammals, including other primates—accounts for 3% of their diet. The maximum life span in the wild is 50 years (Robson and Wood, 2008).

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 will 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 (Varki and Altheide, 2005; Smithsonian Institution, n.d.).



Chimpanzee (*Pan troglodytes*)

Location and Population

Chimpanzees are distributed across equatorial Africa, with discontinuous populations from southern Senegal to western Uganda and Tanzania (Oates *et al.*, 2008a).

Chimpanzees are listed in CITES Appendix I, and all four subspecies are categorized as endangered (EN) on the IUCN Red List (Oates *et al.*, 2008a). There are approximately 70,000–116,000 central chimpanzees; 21,300–55,600 western chimpanzees; 200,000–250,000 eastern chimpanzees; and 3,500–9,000 Nigeria–Cameroon chimpanzees. Populations are believed to be declining, but the rate has not yet been quantified.

Decreases in chimpanzee numbers are mainly attributed to increased poaching for the commercial wild meat trade, disease (particularly Ebola) and mechanized logging (which facilitates poaching) (Oates *et al.*, 2008a).

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. Males will cooperate to hunt, but the level of cooperation involved in social hunting activities varies between communities. Chimpanzees are noted for their sophisticated forms of cooperation, such as in hunting and territorial defense.

Gorilla (*Gorilla* species (spp.))

Location and Population

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

Population estimates for the western gorilla range between 140,000 and 160,000, while as few as 300 Cross River gorillas remain (Oates *et al.*, 2008a). All gorillas are listed as critically endangered (CR) on the IUCN Red List, except for the endangered (EN) Grauer's gorilla, whose status will be reviewed in 2015. Population estimates for Grauer's gorilla are between 2,000 and 10,000 (Robbins and Williamson, 2008). Estimates for the mountain gorilla are between 780 and 880 individuals (Roy *et al.*, 2014b). The main threats to both species are poaching for the commercial wild meat trade, habitat destruction and disease (the Ebola virus in particular) (Robbins and Williamson, 2008; Walsh *et al.*, 2008).

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 is predominantly 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 as well as animal supplements in the form of ants and termites; gorillas do not eat meat. Mountain gorillas are largely herbivorous, feeding 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), whereas eastern gorillas are polygynous and can be polygynandrous, with one or more silverbacks, multiple females, their offspring and immature relatives. Eastern gorillas can live in groups of up to 65 individuals, whereas the maximum group size for the western gorilla is 22. Western gorillas are not territorial and home ranges overlap extensively. Chest beats and vocalizations are used when neighboring silverbacks

come into contact, but mutual avoidance is normally the adopted strategy. Gorillas have also been known to adopt offspring from other females (orphans usually) and raise them as their own (Smuts *et al.*, 1987).

Orangutan (*Pongo* spp.)

Location and Population

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, 2012). Survey data indicate that in 2004 there were approximately 6,500 remaining Sumatran orangutans and at least 54,000 Bornean orangutans (Wich *et al.*, 2008). As a result of continuing habitat loss, the Sumatran orangutan is classified as critically endangered (CR) and the Bornean orangutan as endangered (EN) (Ancrenaz *et al.*, 2008; Singleton, Wich and Griffiths, 2008). Both species are listed in Appendix I of CITES. The main threats to the species are habitat loss, killings due to human–ape conflict, hunting and the international pet trade (Wich *et al.*, 2008; Gaveau *et al.*, 2014).

Physiology

Adult males can reach a height of 94–99 cm and weigh 60–85 kg (flanged) or 30–65 kg (unflanged). Females reach a height of 64–84 cm and weigh 30–45 kg, meaning that orangutans are highly sexually dimorphic. Sumatran orangutans are generally slighter than their Bornean relatives. In the wild, males have a life expectancy of 58 years and females 53 years.

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 termed "unflanged" males. Orangutans are the only great ape to exhibit bimaturism.

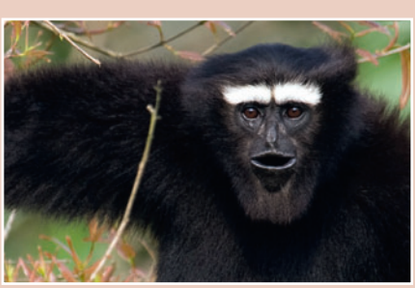
Their diet mainly consists of fruit, but they also eat leaves, shoots, seeds, bark, pith, flowers, eggs, soil and invertebrates (termites and ants). Carnivorous behavior has also been observed, but at a low frequency (preying on species such as slow lorises).

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 *et al.*, 2009b). While females are usually relatively tolerant of each other, flanged males are intolerant of other flanged and unflanged males (Wich *et al.*, 2009b). Orangutans on Sumatra are generally more social than those on Borneo and live in overlapping home ranges, with flanged males continually emitting "long calls" to alert others to their location (Delgado and van Schaik, 2000; Wich *et al.*, 2009b). 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, 2009b).

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

All four genera of gibbon generally share ecological and behavioral attributes, such as monogamy in small territorial groups; vocalization through elaborate song (including complex duets); frugivory and brachiation (moving through the canopy using only the arms). Due to their dependence on fruit, gibbons rarely have multi-female groups (polygyny) and instead remain in small monogamous groups with few offspring. They are diurnal and sing at sunrise and sunset, with a significant part of their day dedicated to finding fruit trees within their territories.



Hoolock genus

Location and Population

There are two species within the Hoolock genus: the western hoolock (*Hoolock hoolock*) and the eastern hoolock (*Hoolock leuconedys*). A new subspecies of the western hoolock was discovered in 2013: the Mishmi Hills

hoolock (*Hoolock hoolock mishmiensis*) (Choudhury, 2013). The western hoolock's distribution spans Bangladesh, India and Myanmar. The eastern hoolock's distribution is in China, India and Myanmar. With an estimated population of 2,500 individuals, the western hoolock is listed as endangered (EN) on the IUCN Red List. The population of eastern hoolock is much higher at 293,200–370,000, and it is listed as vulnerable (VU) 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 for medicinal purposes.

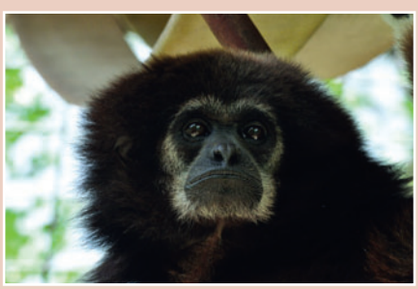
Physiology

The hoolock's head and body length ranges between 45 and 81 cm; they 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. The eastern hoolock also differs from its western counterpart in its pelage, in particular because they have complete separation between the white brow markings and a white preputial tuft.

The diet of the 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

Location and Population

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

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). The overall estimated minimum population for the *Hylobates* genus is about 360,000, with the least abundant species being the moloch gibbon, and most abundant being, collectively, the 'gray gibbons' (Müller's, Abbott's and Bornean gray gibbons). All species are listed as endangered (EN) on the IUCN Red List and are in CITES Appendix I. A number of hybrids of these species occur naturally and continue to coexist with the unhybridized species in the wild. The main collective threats facing the *Hylobates* genus are deforestation, hunting and the illegal pet trade.

Physiology

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

Gibbons are mainly frugivorous, with figs being an especially important part of their diet, 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 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 toward other males, whereas females tend to lead daily movements and ward off other females.

Nomascus genus

Location and Population

Seven species exist in the *Nomascus* genus. See Table AO1: Great apes and gibbons.

The *Nomascus* genus is somewhat less widely distributed than the *Hylobates* genus, being present in Cambodia, Lao PDR, Vietnam and southern China (including Hainan Island). Population estimates exist for some taxa: there are approximately 1,500

western black crested gibbons, 130 Cao Vit gibbons and 23 Hainan gibbons. Population estimates for the white-cheeked gibbons are not available except for some sites, yet overall numbers are known to be severely depleted. The yellow-cheeked gibbons have the largest populations among the *Nomascus* gibbons. All species are listed in CITES Appendix I, with four listed as critically endangered (CR) on the IUCN Red List, two as endangered (EN) and one (*Nomascus annamensis*) yet to be assessed (IUCN, 2014b). 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; they weigh around 7 kg. All *Nomascus* species have sexually dimorphic pelage, with adult males being 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.

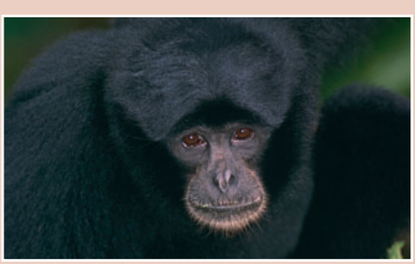
Social Organization

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. Extra-pair copulations outside monogamous pairs have been recorded, although infrequently.

Symphalangus genus

Location and Population

Siamang (*Symphalangus syndactylus*) are found in several forest blocks across Indonesia, Malaysia and Thailand; the species faces severe threats to its habitat across its range. No accurate estimates exist for the total population size. The species is present in CITES Appendix I and is listed as endangered (EN) 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, but the pelage is the same across sexes. The pelage is black, and the species has a large inflatable throat sac.

The siamang's diet relies heavily on figs and somewhat less on leaves, which allows it 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.

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Ape Socioecology

This section presents an overview of the socioecology of the seven species of non-human apes: bonobos, chimpanzees, gibbons (including siamangs), eastern and western gorillas, and Bornean and Sumatran orangutans. For more detailed information, see Wich *et al.* (2009b), Emery Thompson and Wrangham (2013), Reinartz, Ingmanson and Vervaecke (2013), Williamson and Butynski (2013a, 2013b), and Williamson, Maisels and Groves (2013).

Gorillas 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 across 21 countries (Oates *et al.*, 2008a). Orangutans are found in Asia—in both Indonesia and Malaysia—and are the only ape to have two distinct male types. Gibbons are the most numerous of the apes, with 19 species across Asia and Southeast Asia.

Great Ape Socioecology

Social organization differs considerably across the three great ape genera.

Both 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 comprise 10–120 individuals.

Gorillas live in family groups. Their large body size and largely vegetation-based diet enable them to cope with fruit shortages and to maintain stable groups. The median group size is ten: one or more adult "silverback" males with several females and their offspring.

Orangutans are semi-solitary and have loosely defined communities. Flanged adult males, characterized by fatty cheek pads and large size, lead a semi-solitary existence

BOX AO1

IUCN Red List Categories and Criteria, and CITES Appendices

The IUCN Species Survival Commission has defined various categories for each species and subspecies (IUCN, 2012). The criteria can be applied to any taxonomic unit at or below the species level. In order to be ascribed a specific definition, a taxon must fulfil a number of criteria. As all great apes and gibbons are placed within the categories of vulnerable, endangered or critically endangered, this text box presents details on a selection of the criteria for these three categories. Full details of the IUCN Red List Categories and Criteria (in English, French and Spanish) can be viewed and downloaded at: http://jr.iucnredlist.org/documents/redlist_cats_crit_en.pdf. Detailed guidelines on their use can also be seen at: http://www.iucnredlist.org/documents/RedListGuidelines.pdf.

A **vulnerable** (VU) taxon is considered to be facing a high risk of extinction in the wild. It will number fewer than 10,000 mature individuals and there will be evidence of continuing decline and a significant reduction (upwards of 50%) in the size of the population over the past ten years or three generations.

An **endangered** (EN) taxon is considered to be facing a very high risk of extinction in the wild. It will number fewer than 2,500 mature individuals and there will be evidence of continuing decline as well as a significant reduction (upwards of 50%) in the size of the population over the past ten years or three generations.

A **critically endangered** (CR) taxon is considered to be facing an extremely high risk of extinction in the wild. It will number fewer than 250 mature individuals and there will be evidence of continuing decline and a significant reduction (upwards of 80%) in the size of the population over the past ten years or three generations.

CITES Appendices I, II and III to the Convention are lists of species afforded different levels or types of protection from overexploitation.

All non-human apes are listed in **Appendix I**, which includes species that are the most endangered among CITES-listed animals and plants. They are threatened with extinction and 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 the granting of 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 go to: http://www.cites.org/eng/app/.

Table AO1

Great Apes and Gibbons (adapted from Mittermeier *et al.*, 2013)

GREAT APES		
***Pan* genus**		
Bonobo	*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*	■ Benin ■ Burkina Faso ■ Gambia ■ Ghana ■ Guinea ■ Mali ■ Senegal ■ Sierra Leone ■ Togo
***Gorilla* genus**		
Cross River gorilla	*Gorilla gorilla diehli*	■ Cameroon ■ Nigeria
Grauer's gorilla (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 ▸

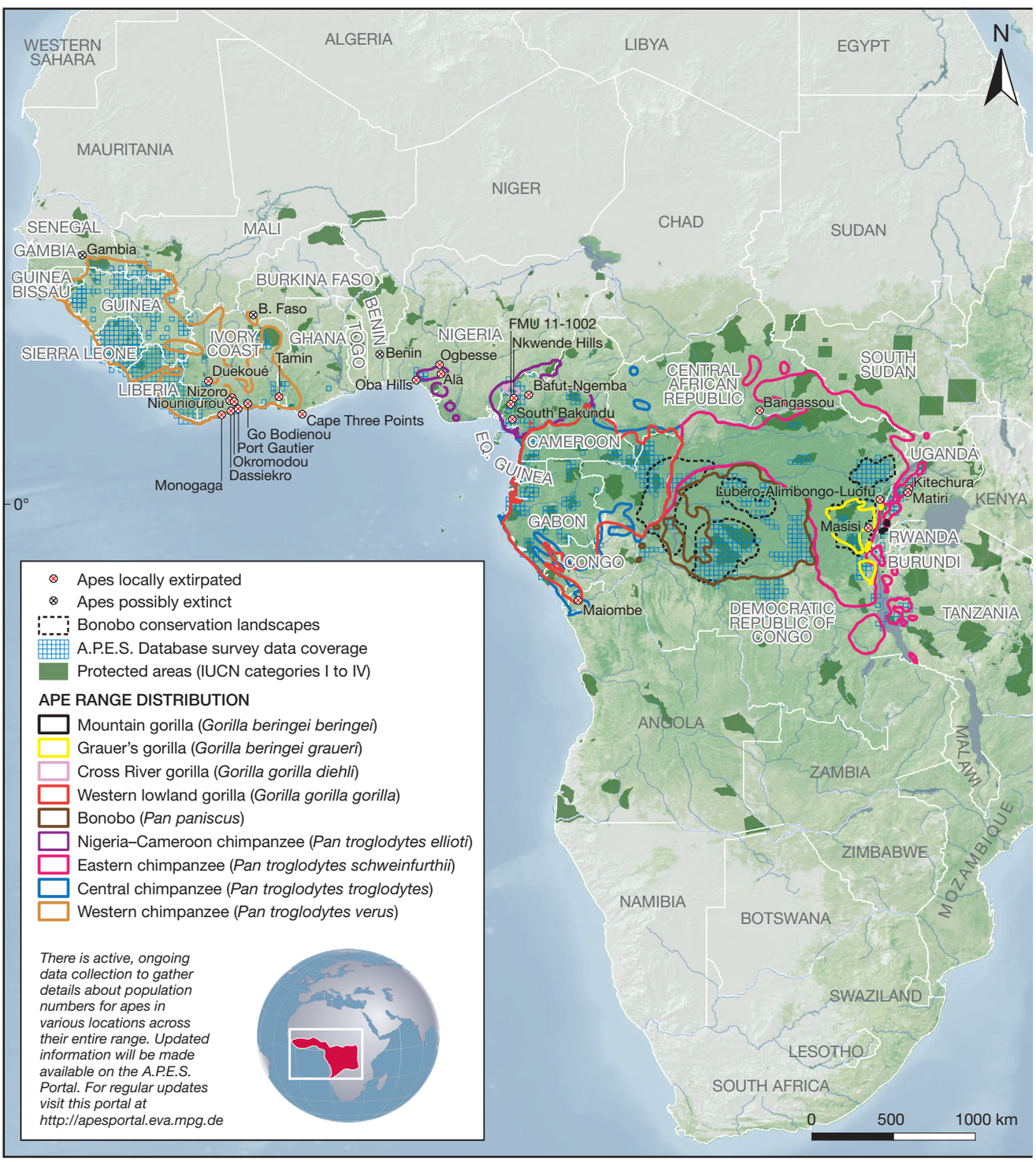
Table AO1

Continued

GIBBONS (excluding subspecies)		
***Hoolock* genus**		
Eastern hoolock	*Hoolock leuconedys*	■ China ■ Myanmar
Western hoolock	*Hoolock hoolock*	■ Bangladesh ■ India ■ Myanmar
***Hylobates* genus**		
Abbott's gray gibbon	*Hylobates abbotti*	■ Indonesia ■ Malaysia
Agile gibbon	*Hylobates agilis*	■ Indonesia ■ Malaysia
Bornean gray gibbon	*Hylobates funereus*	■ Indonesia ■ Malaysia ■ Brunei Darussalam
Bornean white-bearded gibbon	*Hylobates albibarbis*	■ Indonesia
Kloss's gibbon	*Hylobates klossii*	■ Indonesia
Lar gibbon	*Hylobates lar*	■ China ■ Indonesia ■ Lao People's Democratic Republic ■ Malaysia ■ Myanmar ■ Thailand
Moloch gibbon	*Hylobates moloch*	■ Indonesia
Müller's gibbon	*Hylobates muelleri*	■ Indonesia
Pileated gibbon	*Hylobates pileatus*	■ Cambodia ■ Lao People's Democratic Republic ■ Thailand
***Nomascus* genus**		
Cao Vit gibbon	*Nomascus nasutus*	■ China ■ Viet Nam
Hainan gibbon	*Nomascus hainanus*	■ China (Hainan Island)
Northern white-cheeked crested gibbon	*Nomascus leucogenys*	■ Lao People's Democratic Republic ■ Viet Nam
Northern yellow-cheeked crested gibbon	*Nomascus annamensis*	■ Cambodia ■ Lao People's Democratic Republic ■ Viet Nam
Southern white-cheeked crested gibbon	*Nomascus siki*	■ Lao People's Democratic Republic ■ Viet Nam
Southern yellow-cheeked crested gibbon	*Nomascus gabriellae*	■ Cambodia ■ Lao People's Democratic Republic ■ Viet Nam
Western black-crested gibbon	*Nomascus concolor*	■ China ■ Lao People's Democratic Republic ■ Viet Nam
***Symphalangus* genus**		
Siamang	*Symphalangus syndactylus*	■ Indonesia ■ Malaysia ■ Thailand

Figure AO1

Ape Distribution in Africa



(Emery Thompson, Zhou and Knott, 2012). Smaller, unflanged adult males are comparatively tolerant of other orangutans, and adult females sometimes travel together for a few hours to several days. Sumatran orangutans occasionally congregate when food is abundant (Wich *et al.*, 2006).

Ecology

Most great apes live in closed, moist, mixed tropical forest, occupying a range of forest types, including lowland, swamp, seasonally inundated, gallery, coastal, submontane, montane and secondary regrowth. Eastern and western chimpanzees also live in savannah–mosaic landscapes. The largest populations are found below 500 m elevation, in the vast swamp forests of Asia and Africa (Morrogh-Bernard *et al.*, 2003; Stokes *et al.*, 2010), although eastern chimpanzees and eastern gorillas range above 2,000 m altitude. Most chimpanzees inhabit evergreen forests, but some populations exist in deciduous woodland and drier savannah-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 (Kormos *et al.*, 2003; Brncic, Amarasekaran and McKenna, 2010; Tweh *et al.*, 2014).

Great apes are adapted to a plant diet, but all taxa consume insects, and some kill and eat small mammals. Succulent fruits are their main source of nutrition, except at altitudes where few fleshy fruits are available (Watts, 1984). 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).

Gorillas inhabit a broad range of habitats across ten African countries. One commonality of gorillas across their range is that they 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 (Ganas *et al.*, 2004; Doran-Sheehy *et al.*, 2009; Masi, Cipolletta and Robbins, 2009; 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 (Watts, 1984), the only habitat in which gorillas eat almost no fruit as it is virtually unavailable; these conclusions were adjusted once detailed studies were conducted on lowland gorillas. While gorillas incorporate a notable amount of fruit into their diets when it is available (Watts, 1984), they are less frugivorous than chimpanzees, preferring vegetative matter even at times of high fruit availability (Morgan and Sanz, 2006; Yamagiwa and Basabose, 2009; Head *et al.*, 2011).

The distance travelled per day by gorillas declines with increasing availability of understory vegetation, varying between approximately 500 m and 3 km per day. 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 savannah or gallery forests inhabited by chimpanzees.

Chimpanzees eat mainly fruit, although they present 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, 2011b). Chimpanzees are both terrestrial and arboreal; they live in multi-male–multi-female, fission–fusion communities. A single community will change size by fissioning into smaller parties according to resource

Figure AO2

Ape Distribution in Asia

Apes locally extirpated
A.P.E.S. Database survey data coverage
Protected areas (IUCN categories I to IV)

APE RANGE DISTRIBUTION

Gibbons

- Abbott's gray gibbon (*Hylobates abbotti*)
- Agile gibbon (*Hylobates agilis*)
- Bornean white-bearded gibbon (*Hylobates albibarbis*)
- Bornean gray gibbon (*Hylobates funereus*)
- Kloss's gibbon (*Hylobates klossii*)
- Lar gibbon (*Hylobates lar*)
- Moloch gibbon (*Hylobates moloch*)
- Müller's gibbon (*Hylobates muelleri*)
- Pileated gibbon (*Hylobates pileatus*)
- Western hoolock (*Hoolock hoolock*)
- Eastern hoolock (*Hoolock leuconedys*)
- Northern yellow-cheeked crested gibbon (*Nomascus annamensis*)
- Western black-crested gibbon (*Nomascus concolor*)
- Southern yellow-cheeked crested gibbon (*Nomascus gabriellae*)
- Hainan gibbon (*Nomascus hainanus*)
- Northern white-cheeked crested gibbon (*Nomascus leucogenys*)
- Cao Vit gibbon (*Nomascus nasutus*)
- Southern white-cheeked crested gibbon (*Nomascus siki*)
- Siamang (*Symphalangus syndactylus*)

Orangutans

- Sumatran orangutan (*Pongo abelii*)
- Bornean orangutan (*Pongo pygmaeus*)
- Bornean orangutan subspecies boundaries

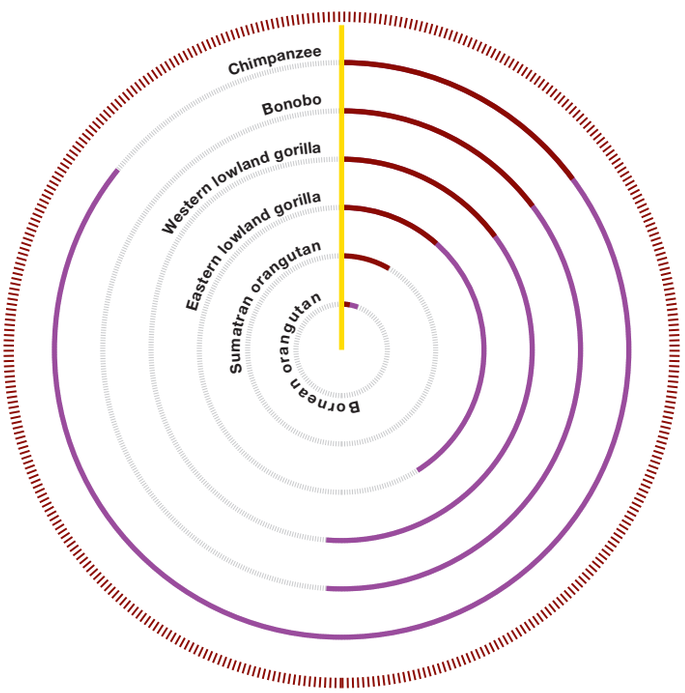
There is active, ongoing data collection to gather details about population numbers for apes in various location across their entire range. Updated information will be made available on the A.P.E.S. Portal. For regular updates visit this portal at http://apesportal.eva.mpg.de

availability and activity (food and access to reproductive females). Parties thus tend to be smaller during periods of fruit scarcity. The most common aggregations are a mixture of males and females with immature offspring. Communities living in forest habitats have annual home ranges of 7–32 km², while in savannah woodland, they range over much wider areas, often exceeding 65 km². Typically, the community's home range is defended by highly territorial males who patrol boundaries and may attack, and even kill, members of neighboring communities. Adult female chimpanzees often spend time alone with their offspring or in a party with other females.

Great apes not only feed, but also rest, socialize and sleep in trees. Being large-brained, highly intelligent mammals, they need long periods of sleep and build nests in which they spend the night. These beds are usually constructed high in 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. They are not adapted for terrestrial locomotion, although Bornean orangutans also travel on the ground in both primary and degraded habitat (Loken, Spehar and Rayadin, 2013; Ancrenaz *et al.*, 2014b). More or less restricted to the canopy, orangutans do not travel great distances on average. 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 (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; chimpanzees travel 2–3 km, with occasional 10 km excursions. Savannah-dwelling chimpanzees generally range farther daily than their forest-dwelling counterparts. See Figure AO3.

Figure AO3

Daily Distances Travelled by Great Apes



Key

Chimpanzee = 2,000–10,000 m
Bonobo = 2,000–6,000 m
Western lowland gorilla = 2,000–6,000 m
Eastern lowland gorilla = 1,500–5,000 m
Sumatran orangutan = flanged 1,000 m, unflanged unknown
Bornean orangutan = flanged 200 m, unflanged 400 m

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 an individual or group 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. The area used habitually by an individual, group or community of a species is referred to as a home range. The establishment of a home range helps a species to secure access to resources within it (Delgado, 2010).

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 so may temporarily reside in a relatively small area (4–8 km² for Bornean males). Orangutan home-range overlap is usually extensive, but flanged male orangutans establish personal space by emitting long calls (see Figure AO4). 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).

Eastern gorillas range over areas of 6–34 km² (Williamson and Butynski, 2013a), and western gorilla home ranges average 10–20 km²—and potentially up to 50 km² (Head *et al.*, 2013). Gorillas are not territorial and neighboring groups' ranges may overlap (see Figure AO4). Encounters between groups can occur without visual contact; instead, silverback males exchange vocalizations and chestbeats until one or both groups move away. Groups are less vigilant of each other in large swampy clearings where good visibility allows silverbacks to monitor potential competitors from a distance (Parnell, 2002). In contrast, other research finds that mountain gorillas engaged in contact aggression during 17% of studied group encounters (Sicotte, 1993). Physical aggression is rare, but if contests escalate, fighting between silverbacks can be intense. Infections of injuries sustained during intergroup interactions and subsequent deaths have occurred (Williamson, 2014).

Chimpanzees living in forest habitats have home ranges of 7–41 km² (Emery Thompson and Wrangham, 2013), and more than 65 km² in savanna (Pruetz and Bertolani, 2009). Male chimpanzees are highly territorial and patrol the boundaries of their ranges (see Figure AO4). Parties of males

may attack members of neighboring communities and some populations are known for their aggression (Williams *et al.*, 2008). Victors benefit by gaining females or increasing the size of their range. Bonobo communities share home ranges of 22–58 km² (Hashimoto *et al.*, 1998). Bonobos exhibit neither territorial defense nor cooperative patrolling; encounters between members of different communities are characterized by excitement rather than conflict (Hohmann *et al.*, 1999).

Wherever gorillas and chimpanzees are sympatric, dietary divisions between the species limit direct competition for food. If the area of available habitat is restricted, such mechanisms for limiting competition will be compromised, but it is thought that both species are more tolerant of each other when they are both attracted to the same highly preferred food source, especially in times of fruit scarcity (Morgan and Sanz, 2006).

Reproduction

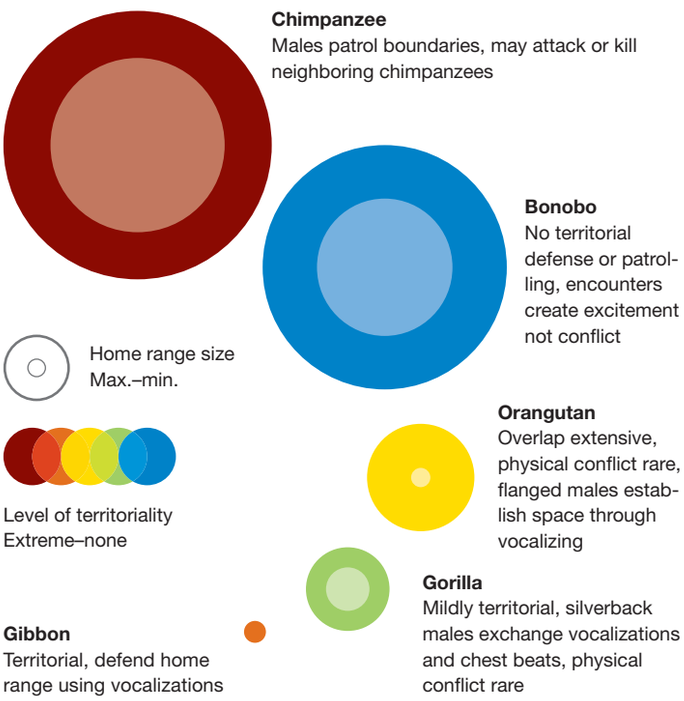
Male apes reach sexual maturity between the ages of 8 and 16 years, with chimpanzees attaining adulthood at 8–15 years, bonobos at 10, eastern gorillas around 15 and western gorillas at 18. Orangutan males mature between the ages of 8 and 16 years, but they may not develop flanges for another 20 years (Wich *et al.*, 2004). Female great apes become reproductive 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 an average 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.

Pregnancy length in gorillas and orangutans is about the same as for humans; it is 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 number of conceiving females (Anderson, Nordheim and Boesch, 2006), with contingent peaks in birth rate during particular months (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.*, 2009a). Meanwhile, gorillas, who are less dependent on seasonal foods, show no seasonality in their reproduction.

All great apes reproduce slowly, due to the mother's high investment in a single offspring and the infant's slow development

Figure AO4

Size of Ape Home Ranges and Levels of Territoriality



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 killing of unweaned offspring by a member of the same species (Harcourt and Greenberg, 2001), typically an unrelated adult male. Infanticide has not been observed in orangutans or bonobos, but if a female gorilla or chimpanzee with an infant switches group, her offspring is likely to be killed by a male in her new group, resulting in early resumption of her reproductive cycle (Watts, 1989).

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/adult female/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); similarly, chimpanzees give birth to four offspring, but only 1.5–3.2 survive beyond infancy (Sugiyama and Fujita, 2011).

Key points to be noted are (1) that documenting the biology of long-lived species takes decades of study due to their slow rates of reproduction, and (2) that great ape populations that have fallen off are likely to take several generations to recover (generation time in the great apes is 20–25 years) (IUCN, 2014b). 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.

Gibbon Socioecology

Gibbons are the most diverse and widespread group of apes. Currently, 19 species of gibbon in four genera are recognized: 9 *Hylobates* species, 7 *Nomascus* species, 2 *Hoolock* species and the single *Symphalangus* species (IUCN, 2014b). 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 (non-evergreen) forests. Some members of the *Nomascus* also occur in limestone karst forests and some populations of *Hylobates* live in swamp forest (Cheyne, 2010). Gibbons occur from sea level up to around 1,500–2,000 m above sea level, although this is taxon and location specific; for example, *Nomascus concolor* has been recorded at up to 2,900 m above sea level in China (Fan Peng-Fei, Jiang Xue-Long and Tian Chang-Cheng, 2009). The *Hylobatidae* are heavily impacted by the extent and quality of forest as they are arboreal (Bartlett, 2007), with the exception of the rarely recorded behavior of moving bipedally and terrestrially across forest gaps or to access isolated fruiting trees in more degraded and fragmented habitats.

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, 2008b; Elder, 2009), although siamangs are more folivorous (Palombit, 1997). Reliance on other protein sources, such as insects, birds'

eggs and small vertebrates, is likely 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 (Marshall and Leighton, 2006; Fan Peng-Fei and Jiang Xue-Long, 2008; Lappan, 2009; Cheyne, 2010). Since gibbons are important seed dispersers, their frugivorous nature is significant in maintaining forest diversity (McConkey, 2000, 2005; McConkey and Chivers, 2007).

Each family group maintains a territory that it defends from other groups. Territories average 0.42 km^2 (Bartlett, 2007), but 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. Other studies, however, have revealed 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 (Palombit, 1994; Reichard, 1995; Lappan, 2008). Research also indicates that the more northerly *N. nasutus*, *N. concolor* and *N. haianus* commonly form polygynous groups with more than one breeding female (Zhou *et al.*, 2008; Fan Peng-Fei and Jiang Xue-Long, 2010; Fan Peng-Fei *et al.*, 2010). 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 sub-optimal habitats.

Both males and females disperse from their natal groups (Leighton, 1987) and establish their own territories; 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, 2007). Although captive individuals have lived upwards of 40 years, gibbon longevity in the wild is unknown but thought to be considerably shorter. Due to the gibbons' relatively late age of maturation and long interbirth intervals, reproductive lifetime may be only 10–20 years (Palombit, 1992). Population replacement in gibbons is therefore relatively slow.

Acknowledgments

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Photo: Industrial agriculture is a method of intensive crop production that is characterized by large monoculture farms and plantations. © Daniel Beltrá/Greenpeace