State of the Apes

Killing, Capture, Trade and Conservation

The illegal trade in live apes, ape meat and body parts occurs across all ape range states and poses a significant and growing threat to the long-term survival of wild ape populations world-wide. What was once a purely subsistence and cultural activity, now encompasses a global multi-million-dollar trade run by sophisticated trans-boundary criminal networks. The challenge lies in teasing apart the complex and interrelated factors that drive the ape trade, while implementing strategies that do not exacerbate inequality. This volume of *State of the Apes* brings together original research and analysis with topical case studies and emerging best practices, to further the ape conservation agenda around killing, capture and trade.

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

State of the Apes

Series editors

Helga Rainer	Arcus Foundation
Alison White	Arcus Foundation
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 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.

State of the Apes

Killing, Capture, Trade and Conservation

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Foreword

Understanding the impact of human behavior on the environment and the countless species facing serious threats to their survival is critical to developing intelligent and flexible approaches that will enable us to live within our planetary boundaries, sustaining the diversity of life and lives. The *State of the Apes* series brings together data and knowledge about the impact of human activities on apes and their habitat. By identifying potential solutions to avoid or minimise harm, it serves as an important resource for surmounting the many challenges confronting us and all other species on this planet. Across their range, ape populations are declining as a result of habitat loss and degradation, hunting and disease; all ape species face the threat of extinction. Understanding the scope and the impact that killing, capture and trade have on the different ape species across Africa and Asia, and how these threats affect their conservation, as well as the well-being of individual animals, is vital to finding solutions for their protection.

The fourth volume in the *State of the Apes* series focuses on one of the most direct threats to apes: hunting. This activity, which is a threat in almost all areas where non-human apes are found, results in their killing, often with the aim of using their body parts for food, medicine or other purposes, or live capture and trade to keep the animals as pets, for props in the entertainment industry or displayed in collections. All apes are protected under the law in every country where they exist: the killing, capture and trade in apes is therefore illegal. Despite this, apes are hunted in every country where they occur naturally, albeit for different and often complex reasons. In some cases, people hunt for cultural reasons, but often it is motivated by economic drivers, either to earn cash, obtain food or to remove an animal that is perceived as a nuisance, destroying crops.

Apes are among the most charismatic groups of species in tropical forests across Africa and Asia. They are intelligent, sentient, social and emotional beings, and given their close genetic similarity and shared evolutionary history with humans, they are often fascinating to people. This fascination or attraction has been one of the factors that has given rise to the threats apes currently face. It is largely based on their "almost-human" aspect that great apes and gibbons are captured to fuel the entertainment industry and to supply the vibrant pet trade and animal collections.

The impact of hunting on the individual apes concerned are also severe, leading to traumatized animals that experience fear, loneliness, pain, confusion and isolation from other individuals of their species. Most apes are social animals, spending years with their mother and natal group, learning how to survive and interact in the wild. When kept in captivity in artificial, stressful conditions, they experience trauma that lasts a lifetime. The hunting and killing or capture of apes, and their trade, has severe impacts on the conservation of these highly threatened species, who often exist in fragmented populations in forest patches that have already been seriously degraded by industrial agriculture, extractive industries and infrastructure projects. The removal of even a few individuals can have significant impacts on a species' future. Their survival is, quite literally, in our hands.

Nadya Hutagalung

United Nations Environment Program (UNEP) and Great Apes Survival Partnership (GRASP) Ambassador/ TV personality

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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 visit:

- arcusfoundation.org.

Or connect with Arcus at:

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

Great Apes and Gibbons Program

The long-term survival of humans, great apes and gibbons 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 great apes and gibbons, and to strengthen protection from threats to their habitats. The Arcus Great Apes and Gibbons Program supports conservation and policy advocacy efforts that promote their survival 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. 282.

Annexes

All annexes can be found at the back of the book, starting on p. 263, 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. 285.

Chapter cross-referencing

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

Ape Abundance Estimates

Definitive, up-to-date abundance estimates are not available for all ape species. The most recent Abundance Annex, which can be accessed at stateoftheapes.com, presents estimates at the site level and uses abundance classes to indicate population ranges. In this volume, the Apes Overview and some chapters feature abundance information based on other geographic scales, drawn from a variety of sources, including forthcoming Red List assessments. Consequently, some figures may not align exactly.

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

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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.

Acknowledgments

As with all volumes in the *State of the Apes* series, pulling together the content for this publication has been an extensive undertaking. Our aim is not only to encourage the critical engagement of all stakeholders, including conservation organizations, civil society, industry, donor and financial institutions, and governments, but also to increase support for great apes and gibbons. We would like to express our gratitude to everyone who played a role, from those who attended our stakeholder meeting, to our contributors and reviewers, to all those involved in the production and translation of the book. Thank you for your input, knowledge, advice, expertise, support, flexibility and patience!

Jon Stryker and the Arcus Foundation Board of Directors have been instrumental in enabling us to produce this publication series. We thank them for their ongoing support of our efforts to bring an overview of critical ape conservation issues to important audiences. We also thank Katrina Halliday and the team at Cambridge University Press for their commitment to this series.

In addition to the thematic content, each publication provides an overview of the status of apes, both in their natural habitats and in captivity. We are very grateful 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 conservation action.

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We are grateful to the authors and contributors of this volume, including those who provided essential data. They are named at the end of each chapter. We could not have produced this book without them. We also extend thanks to our reviewers for providing constructive feedback and helping to ensure the quality of individual chapters and the book as a whole. They are: Katharine Abernethy, Graham L. Banes, Elizabeth L. Bennett, Tom Blomley, Luke Bond, Liana Chua, Rosie Cooney, Isabel Esterman, David Favre, Anna Frostic, Jessica Graham, Justin Kenrick, Tien Ming Lee, Peter J. Li, Neil Maddison, Fiona Maisels, Vincent Nijman, Colman O'Criodain, Alex Piel, Rajindra Puri, Cindy Rizzo, Steve Ross, Nadine Ruppert, Judith Shapiro, Willie Shubert, Serge A. Wich, Elizabeth A. Williamson, Karen Winfield and Stefan Ziegler.

Credits appear alongside all photographs in this volume, many of which were generously contributed by the photographers. We are also thankful to the organizations that allowed us to include extracts from previously published books, journals, reports and internal documents.

To ensure that the *State of the Apes* series is accessible to as many stakeholders, decision- and policy-makers as possible, it is published under an open access agreement with Cambridge University Press and translated into multiple languages. This volume will be available in Bahasa Indonesia, Chinese (Mandarin) and French thanks to our translators, graphic designers and proofreaders: Alboum Associates, Nelly Aubaud Davies, Exile: Design & Editorial Services, Xuezhu Huff, MAPgrafix, Anton Nurcahyo, Owlingua, Hélène Piantone, Erica Taube, Beth Varley and Rumanti Wasturini. The *State of the Apes* editions are available in all languages on the dedicated website (stateoftheapes.com); our thanks go to the Arcus Communications team for managing this site, especially Angela Cave, Sebastian Naidoo and Bryan Simmons.

Many others contributed in various ways, such as by providing introductions, anonymous input and strategic advice, or by helping with essential, if sometimes tedious, administrative tasks. We also thank all those who provided much-appreciated moral support.

Helga Rainer, Alison White
and Annette Lanjouw
Editors

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Apes Overview

Apes Index

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

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 Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) 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 reported maximum life span in the wild is 50 years (Hohmann, Robbins and Boesch, 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. 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 up to 100 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 human DNA (Smithsonian Institute, 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 either endangered or critically endangered on the IUCN Red List. There are approximately 114,200–317,000 central chimpanzees (*Pan troglodytes troglodytes*); 17,600–96,700 western chimpanzees (*Pan t. verus*); 170,000–250,000 eastern chimpanzees (*Pan t. schweinfurthii*); and probably fewer than ►

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9,000 Nigeria–Cameroon chimpanzees (*Pan t. ellioti*) (Heinicke *et al.*, 2019; Humle *et al.*, 2016a; Maisels *et al.*, 2016; Oates *et al.*, 2016; Plumptre *et al.*, 2010, 2016a; Strindberg *et al.*, 2018). All populations are believed to be declining, but the rate has not yet been quantified for all (Humle *et al.*, 2016b). An assessment of the rate of population change for the western chimpanzee from 1990 to 2014 found a 6% annual decline, corresponding to a population decline of 80.2% over the study period (Kühl *et al.*, 2017).

Decreases in chimpanzee numbers are mainly attributed to increased poaching for the commercial wild meat trade, habitat loss and degradation, and disease (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. Some communities include 200 species of food items in a diet of fruit supplemented by bark, flowers, fungi, honey, leaves, pith, seeds, shoots and stems, 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 exceeding 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 other members of 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 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*) (see Figure AO1).

Three of the four gorilla taxa are listed as critically endangered on the IUCN Red List (Bergl *et al.*, 2016; Hickey *et al.*, 2018; Maisels *et al.*, 2018; Plumptre *et al.*, 2016b). The first range-wide population estimate for the western lowland gorilla was undertaken in 2013 and gives a total population of nearly 362,000 while as few as 250–300 Cross River gorillas remain in the wild (Bergl *et al.*, 2016; Dunn *et al.*, 2014; Strindberg *et al.*, 2018). The most recent population estimate for Grauer's gorilla is 3,800, which indicates a 77% loss since 1994 (Plumptre *et al.*, 2016c). Mountain gorillas are estimated to number at least 1,000 individuals (Granjon *et al.*, 2020; Hickey *et al.*, 2019). 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) (Maisels, Bergl and Williamson, 2018; Plumptre, Robbins and Williamson, 2019). The Grauer's gorilla is also threatened by civil unrest (Plumptre, Robbins and Williamson, 2019). A predicted threat is the impact of climate change on the gorilla's forest habitats (Maisels, Bergl and Williamson, 2018; Plumptre, Robbins and Williamson, 2019).

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 and females are about half the size of males. Their lifespan ranges from 30 to 40 years in the wild. Mature males are known as "silverbacks" due to the development of a gray saddle on their back when they attain 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 tree leaves and bark;

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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. Groups that live in the same areas normally adopt a strategy of mutual avoidance.

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 14,000 Sumatran orangutans (*Pongo abelii*) and around 100,000 Bornean orangutans (*Pongo pygmaeus* spp.) remained in the wild (Ancrenaz *et al.*, 2016; GRASP and IUCN, 2018; Singleton *et al.*, 2017; Voigt *et al.*, 2018; 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.*, 2017). 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). 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.*, 2019). It is classified as critically endangered (Nowak *et al.*, 2017)

The main threats to all orangutan species are habitat loss and fragmentation, and killings due to human–ape conflict, hunting and the international live animal trade (Ancrenaz *et al.*, 2016; Gaveau *et al.*, 2014; Singleton *et al.*, 2017; Wich *et al.*, 2008). For the Bornean orangutan, additional threats include forest fires and people's lack of awareness that they are protected by law (Ancrenaz *et al.*, 2016). 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 the Leuser Ecosystem as 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.*, 2017). For the Tapanuli orangutan, industrial development poses a serious threat, from gold and silver mining and existing extensive logging permits, to proposed hydroelectric projects (Nowak *et al.*, 2017; Wich *et al.*, 2019).

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 they are far smaller than males and that orangutans are highly sexually dimorphic. In the wild in Sumatra, the life expectancy is 58 years for males and 53 years for females. 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 consists mainly of fruit, but they also eat leaves, shoots, seeds, bark, pith, flowers, eggs, soil and invertebrates such as 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 and taxa; they are more common in the two Sumatran

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species than the Bornean species. While females are usually relatively tolerant of each other, flanged males are intolerant of other flanged and unflanged males (Wich, de Vries and Ancrenaz, 2009). 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, de Vries and Ancrenaz, 2009). Orangutans are characterized by an extremely slow life history, with the longest interbirth interval of any primate species, an average of 7.6 years (van Noordwijk *et al.*, 2018).

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; Fan, Turvey and Bryant, 2019). 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 and Myanmar (see Figure AO2). To date, the Gaoligong hoolock has only been seen in eastern Myanmar and southwestern China (Fan *et al.*, 2017). The Gaoligong hoolock comprises an estimated nine subpopulations and about 200 individuals in China. No recent population estimates exist for Myanmar (P.-F. Fan, personal communication, 2019). Previous, unconfirmed estimates—dating from the time when the Gaoligong hoolock was still identified as the eastern hoolock—suggest that, in 2009, Myanmar may have been home to as many as 40,000 individuals (Geissmann *et al.*, 2013).

With an estimated population of 15,000 individuals, the western hoolock is listed as endangered on the IUCN Red List (Brockelman, Molur and Geissmann, 2019). The eastern hoolock has a population of 10,000–50,000 and is listed as vulnerable on the IUCN Red List (Brockelman and Geissmann, 2019). Both species are listed in CITES Appendix I, with the main threats identified as habitat loss and fragmentation, and hunting for food, pets, tourism and medicinal purposes. The Gaoligong hoolock is categorized as endangered on the IUCN Red List (Fan, Turvey and Bryant, 2019).

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 white preputial tuft and a complete separation between the white brow markings.

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.

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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 (extirpated?), 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 400,000–480,000. The least abundant species is the moloch gibbon (*Hylobates moloch*) and most abundant, collectively, are 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).

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, Lao People's Democratic Republic, Viet Nam and southern China, including Hainan Island (see Figure AO2). Population estimates exist for some taxa: there are approximately 5,000 western black crested gibbons (*Nomascus concolor*), about 200 Cao Vit gibbons (*Nomascus nasutus*) and 23 Hainan gibbons (*Nomascus hainanus*). Population estimates for the white-cheeked gibbons (*Nomascus leucogenys* and *Nomascus siki*) are available for some sites, and overall numbers are known to be severely depleted. The yellow-cheeked gibbons (*Nomascus annamensis* and *Nomascus 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 (*Nomascus concolor*, *nasutus*, *hainanus* and *leucogenys*) and two as endangered (*Nomascus siki* and *N. gabriellae*), while one—the northern yellow-cheeked crested gibbon (*Nomascus annamensis*)—is yet to be assessed (IUCN, 2019). 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.

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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 (Nijman and Geissmann, 2008).

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.

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Ape Socioecology

This section presents an overview of the socioecology of the different non-human apes: bonobos; chimpanzees; eastern and western gorillas; gibbons (including siamangs); and Bornean, Sumatran and Tapanuli orangutans. The information provided in this section is largely drawn from Emery Thompson and Wrangham (2013), Mittermeier, Rylands and Wilson (2013), Reinartz, Ingmanson and Vervaecke (2013), Robbins (2011), Robbins and Robbins (2018), Wich *et al.* (2009), Williamson and Butynski (2013a, 2013b), and Williamson, Maisels and Groves (2013).

Gorillas live in ten Central African countries (Maisels, Bergl and Williamson, 2018; Plumptre, Robbins and Williamson, 2019). Chimpanzees are the most wide-ranging ape species in Africa, occurring across 21 countries, while bonobos are restricted to the Democratic Republic of Congo (DRC) (Fruth *et al.*, 2016; Humle *et al.*, 2016b). Orangutans are found in Asia—in both Indonesia and Malaysia—and are the only ape to have two distinct male types (Ancrenaz *et al.*, 2016; Nowak *et al.*, 2017; Singleton *et al.*, 2017). Gibbons are the most geographically widespread group of apes. Currently, 20 species of gibbon in four genera are recognized across Asia: 9 *Hylobates* species, 7 *Nomascus* species, 3 *Hoolock* species and the single *Symphalangus* species (Fan *et al.*, 2017; IUCN, 2019; Thinh *et al.*, 2010).

Social Organization

Apes vary considerably in their social organization. While orangutans lead semi-solitary

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). A summary of the five criteria is provided in Annex 1. Full details of the IUCN Red List Categories and Criteria (in English, French and Spanish) can be viewed and downloaded at:

https://www.iucnredlist.org/resources/categories-and-criteria.

Detailed guidelines on their use are available at:

https://www.iucnredlist.org/resources/redlistguidelines.

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. CITES prohibits international trade in species that are threatened with extinction, except under specified circumstances, including for certain types of scientific research. Such exceptional trade requires both an import permit and an export permit, or a re-export certificate—which authorities will grant only if they determine that the transfers will not have a negative impact on the survival of the species in the wild, that the specimens to be transferred have been acquired legally and that the trade is not for primarily commercial purposes—so long as the transfers do not contravene national legislation (see Chapters 6 and 8). 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

Principal Criteria for the Red List Categories: 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 (whichever is longer)
Vulnerable	High	<10,000	>30%
Endangered	Very high	<2,500	>50%
Critically Endangered	Extremely high	<250	>80%

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Table AO2

Great Apes and Gibbons

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 ■ South 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
***Gorilla* genus**		
Cross River gorilla	*Gorilla gorilla diehli*	■ Cameroon ■ Nigeria
Grauer’s 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	*Pongo tapanuliensis*	■ Indonesia

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GIBBONS (excluding subspecies)		
***Hoolock* genus**		
Eastern hoolock	*Hoolock leuconedys*	■ China ■ Myanmar
Gaoligong hoolock (a.k.a. Skywalker hoolock)	*Hoolock tianxing*	■ China ■ Myanmar
Western hoolock	*Hoolock hoolock*	■ Bangladesh ■ India ■ Myanmar
***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*	■ Brunei ■ Indonesia ■ Malaysia
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*	■ Indonesia ■ Lao People's Democratic Republic (PDR) ■ Malaysia ■ Myanmar ■ Thailand
Moloch gibbon (a.k.a. Javan gibbon, silvery gibbon)	*Hylobates moloch*	■ Indonesia

lives, some gibbons form family groups with monogamous pairs, and African great apes —bonobos, chimpanzees and gorillas—a part of larger social groupings.

Bonobos and chimpanzees form multi-male and multi-female dynamic communities or groups that can fission into smaller groups (known as parties) or fuse to form larger ones. These parties can vary in size throughout the day and depending on food availability and the presence of reproductively active females (Wrangham, 1986). Parties, especially in chimpanzees, tend to be smaller during periods of fruit scarcity (Furuichi, 2009). Adult female chimpanzees often spend time alone with their offspring or in a party with other females, while adult female bonobos tend to associate more extensively with their adult sons. Chimpanzee communities average 35 members, with some even exceeding 150 members (Mitani, 2009; Mittermeier, Rylands and Wilson, 2013). Bonobo communities usually comprise 30–80 individuals (Fruth, Williamson and Richardson, 2013). In both species, females are typically the dispersing sex, emigrating from their native community to a neighboring one upon sexual maturity, which bonobos reach between the ages of 6 and 13, while chimpanzees do so between the ages of 8 and 14 (Furuichi *et al.*, 1998; Walker *et al.*, 2018).

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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 ■ Viet Nam
Western black crested gibbon (a.k.a. black crested gibbon, black gibbon, concolor gibbon, Indochinese gibbon)	*Nomascus concolor*	■ China ■ Lao PDR ■ Viet Nam
***Symphalangus* genus**		
Siamang	*Symphalangus syndactylus*	■ Indonesia ■ Malaysia ■ Thailand

Sources: Mittermeier, Rylands and Wilson (2013); personal communication in 2019 with Susan Cheyne, Serge Wich and Elizabeth A. Williamson

Gorillas live in stable, cohesive social units, or groups, with a median size of ten. Most groups consist of one or more "silverback" males with several females and their offspring. Mountain gorillas differ, in that they frequently contain more than 20 individuals and have a multi-male structure (Robbins and Robbins, 2018). Their largely vegetation-based diet enables mountain gorillas to live in areas with limited amounts of fruit and to maintain stable groups. Western gorillas typically form one-male groups with one silverback, although multi-male and all-male groups (non-reproductive groups that contain no females) occur occasionally. Multi-male groups contain more than one silverback, but only rarely contain more than two.

Gorillas are among the few primate species in which both males and females disperse from their natal groups. Males emigrate to become solitary when they are blackbacks or young silverbacks (about 13–15 years of age). Males may be solitary for several years before forming a group. Male western gorillas tend to acquire groups around age 18, a few years later than mountain gorillas, who typically become dominant around 15 years of age. Western gorilla males almost exclusively follow the path of becoming solitary and forming new groups when females join them. Mature

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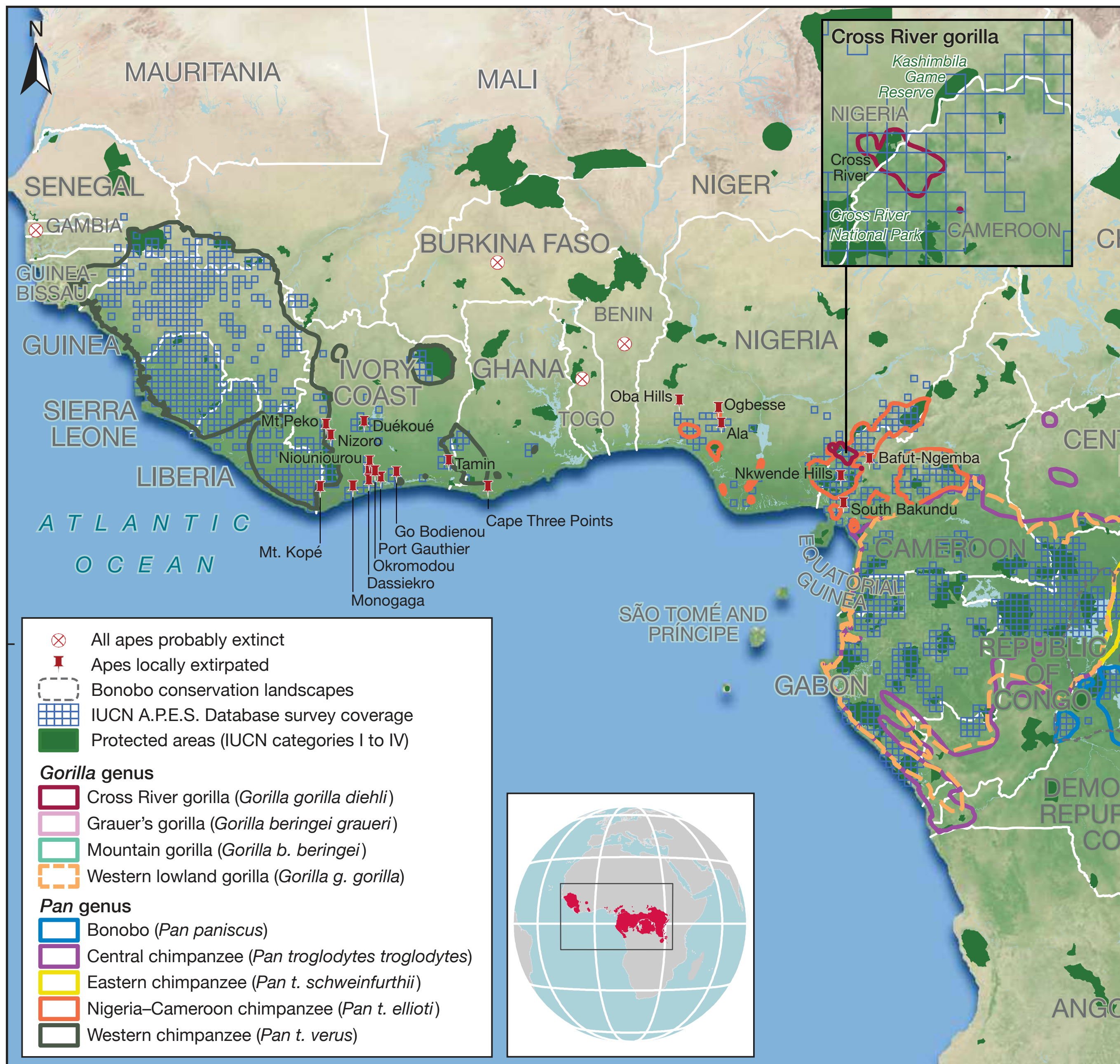
males never join established groups, so multi-male groups are extremely rare among western gorillas. When the silverback of a one-male group dies, the group disintegrates, as the adult females and immature offspring join a solitary male or another group. In contrast to western gorillas, about 40% of mountain gorilla groups are multi-male. Mountain gorilla males follow one of two strategies to become the leader of a

Figure AO1

Ape Distribution in Africa[1]



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group: either they remain in the group and attempt a takeover from within, or they emigrate to become solitary males and eventually form new groups (Robbins and Robbins, 2018).

Note: Active collection of population data is ongoing for apes in various locations across their entire range. Updated information is available on the A.P.E.S. Portal (IUCN SSC, n.d.).

Orangutans are semi-solitary and have loosely defined communities. The basic social unit is a single individual, although adult females are usually found with one baby or one baby and an adolescent. Flanged adult males, characterized by fatty cheek pads and large size, lead a semi-solitary existence and are rather intolerant of other flanged males and, to a lesser degree, unflanged ones (Emery Thompson, Zhou and Knott, 2012; Utami-Atmoko *et al.*, 2009b). Smaller, unflanged adult males are more tolerant of other orangutans. Adult females are the most social individuals and sometimes travel together for a few hours to several days, especially in Sumatra, where orangutans occasionally congregate when food is abundant (Wich *et al.*, 2006). Male orangutans are the dispersing sex: upon reaching sexual maturity, they leave the area where they were born to establish their own range.

Gibbons are highly territorial and live in semi-permanent family groups, defending a territory to the exclusion of other gibbons. Both male and female gibbons disperse from their natal groups and establish their own territories (Leighton, 1987). 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), departure from 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 (Fan and Jiang, 2010; Fan *et al.*, 2010; Zhou *et al.*, 2008). There is no consensus regarding the underlying reasons for these variable social and mating structures; they may be natural or a by-product of small

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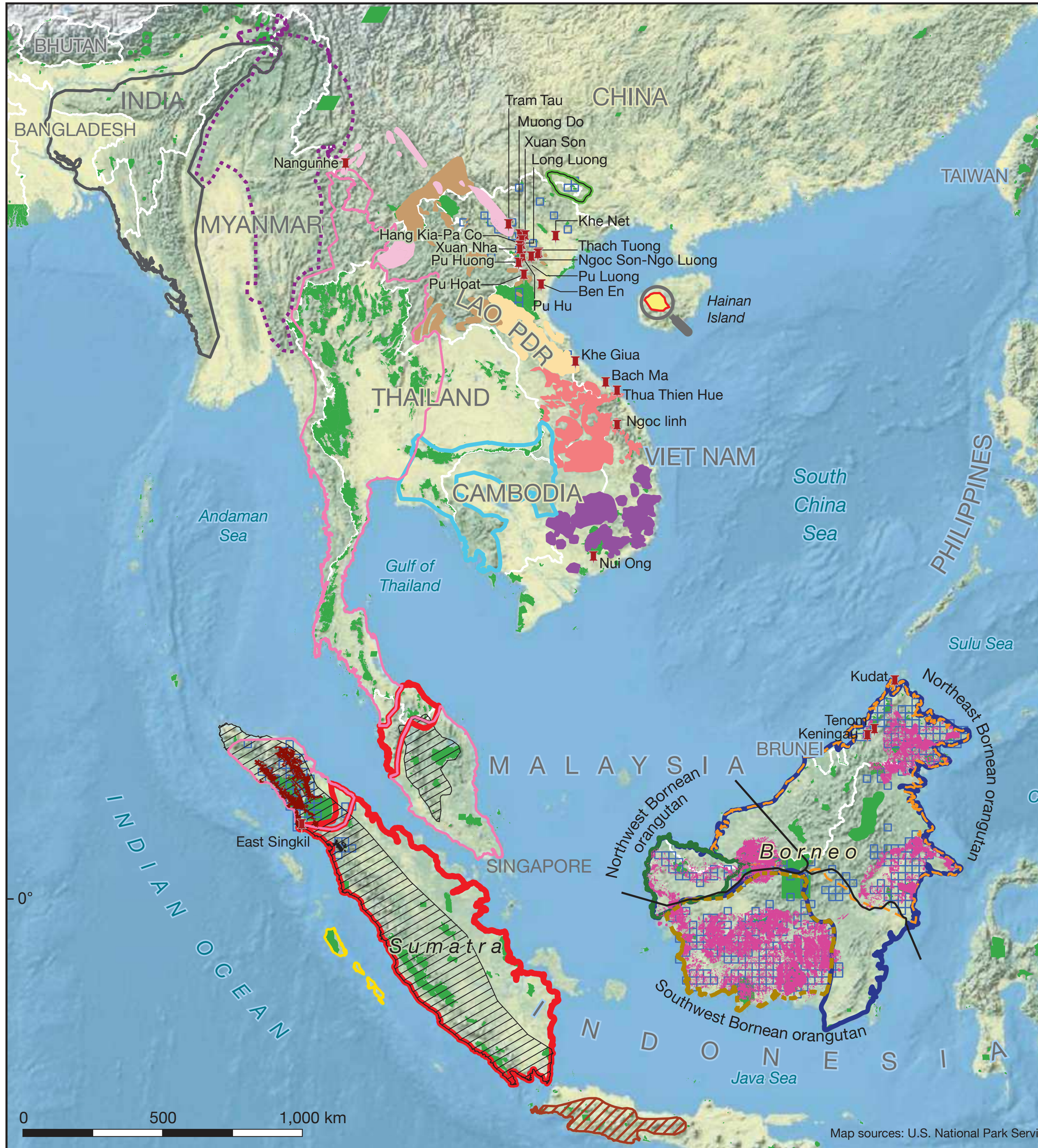
Figure AO2

Ape Distribution in Asia[2]



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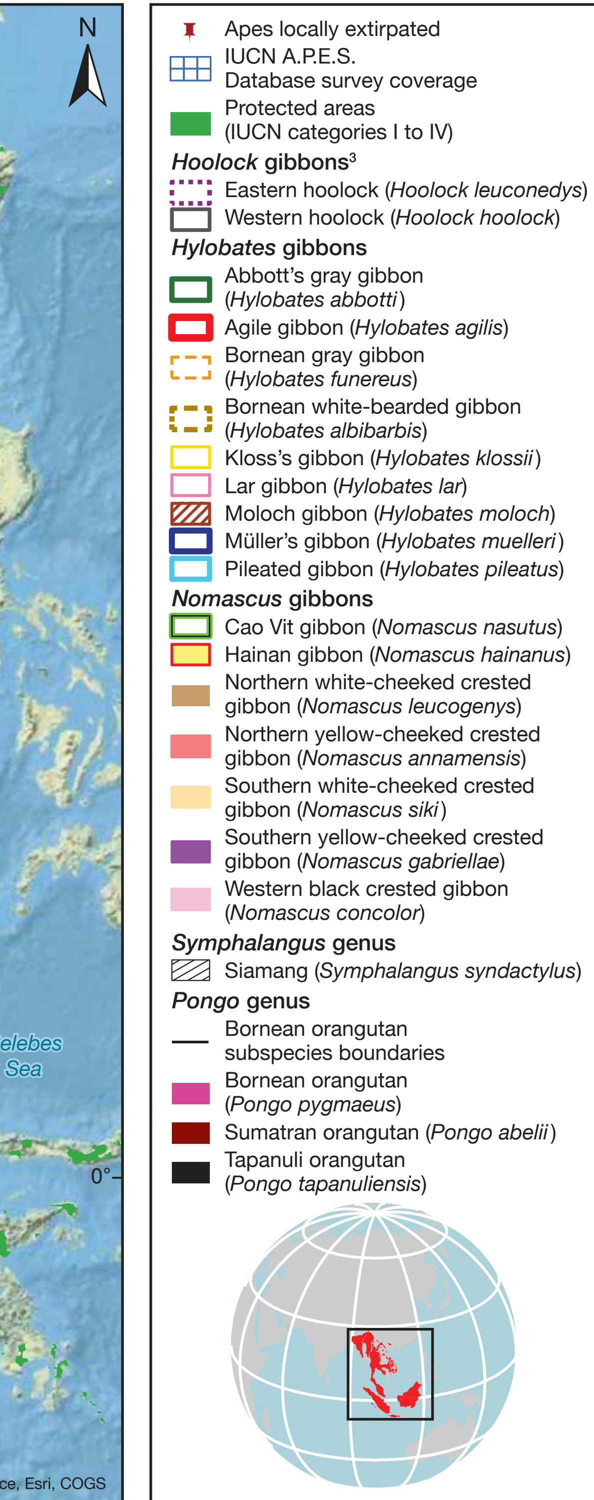

Note: Active collection of population data is ongoing for apes in various locations across their entire range. Updated information is available on the A.P.E.S. Portal (IUCN SSC, n.d.).

population sizes, compression scenarios or suboptimal habitats. Group demography only changes in the event of a death of one of the adults; there is no regular immigration into or emigration from these social groups. Gibbons in fragments are isolated from other groups and thus their dispersal is compromised, which can threaten the long-term sustainability of these populations. There is insufficient information about dispersal distances for sub-adult gibbons to determine maximum distances over which gibbons can disperse (perhaps with assistance of canopy bridges).

Habitat Type and Status

Most 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 forests. Some bonobo populations and eastern and western chimpanzees also live in forest–savannah mosaic landscapes. The largest populations of great apes are found below 500 m elevation, in the vast swamp forests of Asia and Africa (Williamson *et al.*, 2013). Bonobos have a discontinuous distribution at 300–700 m above sea level across undulating terrain in the DRC, south of the Congo River (Fruth *et al.*, 2016; Fruth, Williamson and Richardson, 2013). Eastern chimpanzees and eastern gorillas can range above 2,000 m altitude; orangutans can be found at above 1,000 m in both Sumatra and Borneo (Payne, 1988; Wich *et al.*, 2016; Williamson *et al.*, 2013).

Most chimpanzees and bonobos inhabit evergreen forests, but some populations also 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 occur outside. Indeed, the majority of chimpanzees in

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West Africa—in countries such as Guinea, Liberia and Sierra Leone—are present outside protected areas, and approximately 80% of central chimpanzees and western gorillas live outside of protected areas in Central Africa (Brncic, Amarasekaran and McKenna, 2010; Kormos *et al.*, 2003; Strindberg *et al.*, 2018; Tweh *et al.*, 2015). Nowadays half of the wild orangutan population in Indonesian Borneo is surviving outside of protected forests, in areas that are prone to human development and transformation (Wich *et al.*, 2012b). Gibbons range from montane to lowland peat swamp habitats, up to 1,700 m elevation (Guan *et al.*, 2018). Many gibbons exist outside protected areas (Cheyne *et al.*, 2016; Geissmann *et al.*, 2013; Sarma, Krishna and Kumar, 2015).

Diet

Great apes are adapted to a plant diet, but all taxa consume insects, and some kill and eat small mammals. All apes may also target cultivars—that is, crops in fields or fruit and trees in orchards and plantations—especially when wild foods are scarce, but also because these may be preferred, since they are highly nutritious and easy to access. Succulent fruits are the main source of nutrition for all great apes, except at altitudes where mountain gorillas occur and few fleshy fruits are available. Although mainly fruit eaters, bonobos consume more terrestrial herbaceous vegetation, as well as aquatic plants, than chimpanzees (Fruth *et al.*, 2016). Gorillas across their range 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; these conclusions were adjusted once detailed studies were conducted on gorillas living in lower altitude habitats (Doran-Sheehy *et al.*, 2009; Masi, Cipolletta and Robbins, 2009; Watts, 1984; Wright *et al.*, 2015). While gorillas incorporate a notable amount of fruit into their diets when it is available, they are less frugivorous than chimpanzees, consuming vegetative matter even at times of high fruit availability (Head *et al.*, 2011; Morgan and Sanz, 2006; Yamagiwa and Basabose, 2009).

Mountain gorillas are primarily terrestrial. Although western gorillas are more arboreal, they still primarily travel on the ground and not through the tree canopy. 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). During certain periods of fruit scarcity, African apes concentrate on terrestrial herbs, leaves or bark.

Similarly, in Asia, orangutans feed primarily on fruits, but they consume more bark and young leaves when fruit sources become scarce; orangutans adapt their diet to what is available in the forest. Sumatran orangutans are more frugivorous than their Bornean relatives. In Borneo, they are known to feed on more than 1,500 plant species from 453 genera and 131 families (Russon *et al.*, 2009). The list continues to grow as more data are collected. The resilience of the species and its ability to cope with drastic habitat changes are further illustrated by records of species presence in acacia plantations in East Kalimantan (Meijaard *et al.*, 2010); a mosaic of mixed agriculture in Sumatra (Campbell-Smith

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et al., 2011); oil palm plantations in Borneo (Ancrenaz *et al.*, 2015); and in forests exploited for timber (Ancrenaz *et al.*, 2010; Wich *et al.*, 2016). In these disturbed landscapes, Bornean orangutans rely more on young shoots and leaves than in primary forest.

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 and mature leaves, as well as flowers, although siamangs are more folivorous (Bartlett, 2007; Cheyne, 2008; Elder, 2009; Palombit, 1997). Reliance on other protein sources, such as insects, bird eggs and small vertebrates, is probably underrepresented in the literature. The diet composition changes with the seasons and habitat type; flowers and young leaves dominate during the dry season in peat-swamp forests, while figs dominate in dipterocarp forests (Cheyne, 2010; Fan and Jiang, 2008; Lappan, 2009; Marshall and Leighton, 2006). While gibbons have not been observed to forage on crops (either on plantations or small-scale farms), it is possible that gibbons do exploit disturbed areas if necessary.

Home and Day Range

Foraging in complex forest environments requires spatial memory and mental mapping. Daily searches for food are generally restricted to a particular location, an area of forest that an individual ape 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 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. Establishing a home range helps apes to secure access to resources within it (Delgado, 2010; Mittermeier, Rylands and Wilson, 2013).

Chimpanzee home ranges can vary dramatically, ranging from around 10 to 90 km^2 (1,000–9,000 ha), depending on the habitat and resource distribution; populations in dryer and more open habitats exhibit larger home ranges (Herbinger, Boesch and Rothe, 2001; Pruetz and Herzog, 2017). Male chimpanzees are typically 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). Victors benefit by gaining females or increasing the size of their range. Chimpanzees are generally highly intolerant of neighboring groups and inter-group encounters can result in lethal attacks among males in particular (Mitani, Watts and Amsler, 2010; Watts *et al.*, 2006; Wilson *et al.*, 2014). The frequency of such encounters can be exacerbated by shifts in home ranges linked to habitat loss, changes in habitat quality and disruptions in the chimpanzees' environment (such as road construction or logging).

The home range of bonobos also varies significantly, between 20 and 60 km^2 (2,000–6,000 ha), typically with extensive overlap between the ranges of different communities (Fruth, Williamson and Richardson, 2013). Bonobos do not engage in territorial defense or cooperative patrolling; encounters between members of different communities are more often characterized by excitement rather than conflict (Hohmann *et al.*, 1999).

Eastern gorillas range over areas of 6–34 km^2 (600–3,400 ha), and western gorilla home ranges average 10–20 km^2 (1,000–2,000 ha)—and potentially up to 50 km^2 (5,000 ha) (Caillaud *et al.*, 2014; Head *et al.*, 2013; Robbins, 2011; Seiler *et al.*, 2018; Williamson and Butynski, 2013a, 2013b). Gorillas are not territorial; they have overlapping home ranges that they do not actively defend. There is evidence, however,

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that they have distinct, exclusive core areas (the parts 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, which may lead to increased fighting, injuries and mortality (Caillaud *et al.*, 2014). Encounters between groups can occur without visual contact; instead, silverback males exchange vocalizations and chestbeats until one or both groups move away. Most encounters between groups involve more than auditory contact 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. In some cases, injuries sustained during intergroup interactions have become infected and led to deaths (Rosenbaum, Vecellio and Stoinski, 2016; Williamson, 2014).

A male orangutan's range encompasses several (smaller) female ranges. As high-status flanged males are able to monopolize both food and females to a degree, they may temporarily reside in a relatively small area—4–8 km² (400–800 ha) for Bornean males—even though the actual size of their home range could be much larger than 10 km² (1,000 ha). Orangutan home-range overlap is usually extensive, but flanged male 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).

African apes are semi-terrestrial and often rest on the ground during the daytime; in contrast, orangutans are almost exclusively arboreal, although the Bornean species use terrestrial locomotion more often than previously thought (Ancrenaz *et al.*, 2014). Bornean flanged adult males and adult females move an average of 200 m each day; unflanged adult males usually cover twice that distance. Sumatran orangutans move farther, but still less than 1 km each day on average (Singleton *et al.*, 2009). Orangutans can walk on the ground for considerable distances in all types of natural and human-made habitats, especially in Borneo (Ancrenaz *et al.*, 2014; Loken, Boer and Kasyanto, 2015; Loken, Spehar and Rayadin, 2013). Consequently, they are able to cross open artificial infrastructures to a certain extent. In Sabah, for example, orangutans have been seen crossing sealed and dust roads as long as the traffic is not too heavy. Increased terrestriality in orangutans increases sanitary concerns and the risk of contracting diseases to which they are not usually exposed in the tree canopy. At this stage, there is a dearth of information about such sanitary and health risks.

Territorial apes whose habitats are destroyed encounter great difficulties establishing a new territory nearby, where other animals are already established. Indeed, animals whose territory has been destroyed slowly die off. Unflanged adult males do not seem to have a strictly defined territory and move over large distances (Ancrenaz *et al.*, 2010).

The semi-terrestrial African apes range considerably longer distances and the most frugivorous roam several kilometers each day: mountain gorillas travel about 500 m–1 km per day; bonobos and western lowland gorillas average 2 km but sometimes reach 5–6 km; and chimpanzees travel 2–3 km, although they occasionally venture out on 10-km excursions. Savannah-dwelling chimpanzees generally range farther daily than their forest-dwelling counterparts. The distance travelled by gorillas declines

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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 forest–savannah mosaics or gallery forests inhabited by chimpanzees and bonobos (Robbins, 2011).

Hylobates gibbon territories average 0.42 km² (42 ha), but there is considerable variation. The more northerly *Nomascus* taxa maintain larger territories—from about 0.13 to 0.72 km² (13–72 ha)—possibly in line with lower resource abundance at certain times of year in these more seasonal forests (Bartlett, 2007; Fan *et al.*, 2013). Less seasonal forests have increased resource abundance, yet gibbon density and territory size may not be directly correlated with these factors (Bryant *et al.*, 2015; Hamard, Cheyne and Nijman, 2010; Zhang *et al.*, 2014).

Nesting

Most 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. All great apes build nests or beds in which they spend the night; bonobos and chimpanzees may also build daytime nests in trees or on the ground to rest, while gorillas nest primarily on the ground. All weaned great ape individuals will build a nest to sleep in at night. Tree nests are usually constructed between 10 and 20 m above ground (Fruth, Tagg and Stewart, 2018). Variation in nesting height is influenced by environmental variables such as rainfall, temperature, habitat structure, availability of material, predator presence, and demographic parameters such as the sex or the age of the individual, as well as social factors such as transferred habits (Fruth and Hohmann, 1996). All great apes may reuse nests, although the frequency of reuse depends largely on the availability of sleeping site locations and material for construction (Fruth, Tagg and Stewart, 2018). Bonobos prefer to nest in areas with abundant food, while sleeping site association with fruiting trees is more variable in chimpanzees (Fruth, Tagg and Stewart, 2018; Serckx *et al.*, 2014). However, both chimpanzees and bonobos show preferences when it comes to nesting in specific tree species (Fruth, Tagg and Stewart, 2018).

Reproduction

Male great apes reach sexual maturity between the ages of 8 and 18 years, with chimpanzees attaining adulthood at 8–15 years, bonobos at 10, eastern gorillas around 12–16 and western gorillas at 18 (Williamson *et al.*, 2013). Orangutan males mature between the ages of 8 and 16 years, but they may not develop flanges for another 20 years (Utami-Atmoko *et al.*, 2009a). Female 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 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 (van Noordwijk *et al.*, 2018).

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 months (van Noordwijk *et al.*, 2018; Wallis, 1997). 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

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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, with contingent peaks in birth rate during particular months (Anderson, Nordheim and Boesch, 2006; 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). Meanwhile, gorillas are less dependent on seasonal foods and show no seasonality in their reproduction.

Gibbon 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, and gestation lasts about seven months (Bartlett, 2007). Captive individuals have lived upwards of 40 years; gibbon longevity in the wild is unknown but thought to be considerably shorter. Since gibbons mature relatively late and have long interbirth intervals, their reproductive lifetime may be only 10–20 years (Palombit, 1992). Population replacement in gibbons is therefore relatively slow.

All apes have slow reproductive rates; mothers invest considerable time in a single offspring and infants are slow to develop and mature. Infants sleep with their mothers until they are weaned (4–5 years in African apes; 5–6 years in Bornean orangutans; 7 years in Sumatran orangutans) or a sibling is born. Weaning marks the end of infancy for African apes around the age of 3–6 years, 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 if a member of the same species—typically an unrelated adult male—kills unweaned offspring (Harcourt and Greenberg, 2001; Hrdy, 1979). Infanticide has not been observed in orangutans or bonobos, but if a female gorilla or 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 (Knott *et al.*, 2019; 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 per adult female per year, or one birth for every adult female every 3.3–5.0 years. Mountain gorilla females produce an average of 3.6 offspring during their lifetimes; similarly, chimpanzees produce 1.0–4.3 offspring who survive into adulthood (Emery Thompson, 2013; Robbins *et al.*, 2011).

Key points to be noted are that: 1) documenting the biology of long-lived species takes decades of research due to their slow rates of reproduction, and 2) ape populations that have declined in numbers are likely to take several generations to recover (generation time among apes is 18–25 years) (IUCN, 2019). These factors make 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; as a result, they are the most susceptible to loss (Wich, de Vries and Ancrenaz, 2009; Wich *et al.*, 2009).

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Endnotes

1 The Arcus Foundation commissioned the ape distribution maps (Figures AO1 and AO2) for *State of the Apes*, so as to provide accurate and up-to-date illustrations 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.

2 See Endnote 1.

3 The newly identified Gaoligong or Skywalker hoolock (*Hoolock tianxing*) does not appear on the map, as there is no detailed distribution information for the species. To date, it has only been seen in eastern Myanmar and south-western China.

4 Arcus Foundation (www.arcusfoundation.org/).

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8 Borneo Nature Foundation (www.borneonaturefoundation.org).

9 University of Kent (www.kent.ac.uk/sac).

10 WWF-Vietnam (vietnam.panda.org/).

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12 University of Stirling (www.stir.ac.uk/about/faculties/natural-sciences/).

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Photo: Ape hunting and trade refer to the illegal capture, killing, transport, sale and possession of live apes, their body parts or meat. © Paul Hilton/Earth Tree Images