

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 present only 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' historical 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 36–43 kg, while females are slightly smaller, weighing 26–36 kg. Bonobos are moderately sexually dimorphic and similar in size and appearance to chimpanzees, although with a smaller head and lithier appearance. Their life expectancy in the wild is estimated at about 40 years, while the oldest known captive bonobo was 60 years of age (Hohmann, Robbins and Boesch, 2006; Lowenstine, McManamon and Terio, 2016; 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 the 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 120 individuals, consisting of multiple males and females. When foraging, they split into smaller mixed-sex subgroups, or parties, averaging 5–23 individuals. Male bonobos cooperate with and tolerate one another; however, lasting bonds between adult males are rare, in contrast to the bonds between adult females, which are strong and potentially last for years. A distinguishing feature of female bonobos is that they are co-dominant with males and form alliances against certain males within the community. Among bonobos, the bond between mother and son is the strongest, lasts into the son's adulthood and proves highly important for his social status. During intergroup encounters, bonobos, especially females, tend to exhibit relaxed interactions, such as feeding in the same fruiting tree (Idani, 1990). Female bonobos are the dispersal sex and usually immigrate to neighboring communities (Ishizuka, Toda and Furuichi, 2020). Together with chimpanzees, bonobos are the closest living relatives of humans, with whom they share 98.8% of their DNA (Smithsonian Institute, 2022; The Chimpanzee Sequencing and Analysis Consortium, 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. They can be found in forest-dominated landscapes as well as ones dominated by savannah and agricultural mosaics (Humble *et al.*, 2016; 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 about 114,200–317,000 central chimpanzees (*Pan troglodytes troglodytes*); 17,600–96,600 western chimpanzees (*Pan t. verus*); 170,000–

▶ 250,000 eastern chimpanzees (*Pan t. schweinfurthii*); and probably fewer than 9,000 Nigeria–Cameroon chimpanzees (*Pan t. ellioti*).¹

All populations are believed to be declining, but the rate has not yet been quantified for all (Humble *et al.*, 2016b). The western chimpanzee population decreased at a rate of 6% per year from 1990 to 2014, which corresponds 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 (Humble *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 60 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, 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 small number of individuals staying together for a few days before rejoining other members of the community.

Home ranges are typically 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. Female chimpanzees are the dispersal sex and usually immigrate to a neighboring community during adolescence or in early adulthood. Chimpanzees are noted for their ability to use tools, especially to access embedded foods such as termites or the kernel of a nut, and for their sophisticated forms of cooperation, such as in hunting and territorial defense. The level of cooperation in social hunting activities and their tool-use repertoire vary 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.² The first range-wide population estimate for the western lowland gorilla put the total population at nearly 362,000 in 2013; since then, the figure

has decreased considerably. In 2018 scientists estimated that by 2020 the total population would be just 300,000 (Strindberg *et al.*, 2018; Williamson, Strindberg and Maisels, 2018). As few as 250–300 Cross River gorillas remain in the wild (Bergl *et al.*, 2016; Dunn *et al.*, 2014). The most recent population estimate for Grauer's gorilla is 6,800, which is up from the 2016 estimate due to improvements in the accuracy of assessments, but still indicates an overall loss of 60% and in the Kahuzi-Biega National Park, a loss estimated at 80%, since the mid-1990s (Maisels, Plumptre and Strindberg, 2021; Plumptre *et al.*, 2021). An estimated 1,000 mountain gorillas remain in the wild (Granjon *et al.*, 2020b; Hickey *et al.*, 2019a).

The main threats to both the eastern and western gorilla 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). Grauer's gorilla is also threatened by civil unrest (Plumptre, Robbins and Williamson, 2019). Another 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 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 on their back when they attain maturity.

The gorillas’ diet consists predominantly of ripe fruit, tree leaves and terrestrial, herbaceous vegetation. More herbaceous vegetation is ingested while fruit is scarce, in line with seasonality. 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. Groups that live in the same areas normally adopt a strategy of mutual avoidance. When neighboring silverbacks come into contact, they generally use chest beats and vocalizations, although intergroup encounters can escalate into physical fights.



Orangutan (*Pongo* spp.)

Distribution and Numbers in the Wild

Although orangutans were once present throughout much of southern Asia, their range is now limited to the two islands of Sumatra and Borneo (Delgado and van Schaik, 2000; Wang *et al.*, 2014; see Figure AO2).

In Sumatra in 2015, fewer than 14,000 Sumatran orangutans (*Pongo abelii*) were ranging over 17,000 km² (1.7 million ha), primarily in the Leuser Ecosystem (Singleton *et al.*, 2017). Fewer than 1,000 individuals of the newly described species, the Tapanuli orangutan (*Pongo tapanuliensis*), are found in about 1,000 km² (100,000 ha) of fragmented forests in Batang Toru (Nowak *et al.*, 2017; Wich *et al.*, 2019). In Borneo, between 80,000 and 100,000 Bornean orangutans (*Pongo pygmaeus* spp.) remain in the wild over more than 100,000 km² (10 million ha) (Ancrenaz *et al.*, 2016; Voigt *et al.*, 2018). 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; Nowak *et al.*, 2017; Singleton *et al.*, 2017). All three species are listed in Appendix I of CITES.

The main threats to all orangutan species are habitat loss and fragmentation, as well as killings in the context of human–ape conflict, hunting and the international live animal trade.³ For the Bornean orangutan, additional threats include forest fires and people’s lack of awareness that they are protected by law (Sherman *et al.*, 2020). The main threat to the Sumatran orangutan is the cur-

rent land use plan issued by the government of Aceh, which does not recognize the Leuser Ecosystem’s National Strategic Area status (Singleton *et al.*, 2017). As a result, illegal logging and habitat loss represent high risks to the species’ long-term survival (Wich *et al.*, 2016). The small size of the only remaining population of Tapanuli orangutans is a serious concern as it may lead to inbreeding and genetic depression (Nater *et al.*, 2017). The proposed hydroelectric dam and its associated infrastructure would further fragment and isolate the population by splitting the Sibual-Buali Nature Reserve (Laurance *et al.*, 2020; Nasution, Perwitasari-Farajallah and Utami-Atmoko, 2018, 2020; Wich *et al.*, 2019).

Physiology

Orangutans are highly sexually dimorphic. Adult males can reach a height of 94–99 cm and weigh 60–85 kg (flanged) or 30–65 kg (unflanged). Females are far smaller than males, reaching about 64–84 cm and weighing 30–45 kg. In the wild in Sumatra, the life expectancy is 58 years for males and 53 years for females. Bornean orangutans may live as long, although no accurate data are yet available for this species.

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 mammal species to exhibit male bimaturism.

The orangutan diet consists mainly of fruit, although it also features leaves, shoots, seeds, bark, pith, flowers, eggs, soil and invertebrates, such as termites and ants. Carnivorous behavior has also been observed, especially in Sumatra, but at a very low frequency (preying on species such as slow lorises).

Social Organization

The mother–offspring unit is the only permanent social unit among orangutans. Social interaction between independent individuals does occur, with varying frequency across populations and taxa; they are more common in the two Sumatran species than the Bornean species (Fröhlich *et al.*, 2020; Roth *et al.*, 2020). While females are usually relatively tolerant of each other, flanged males are intolerant of other flanged and unflanged males (Utami-Atmoko *et al.*, 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; Spillmann *et al.*, 2017). 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.)

The four genera of gibbon share ecological and behavioral attributes, such as social monogamy in territorial groups; vocalization through elaborate song (including complex duets); and frugivory and brachiation (moving through the canopy using only the arms). Gibbons primarily consume fruit but have a varied diet that includes insects, flowers, leaves and seeds. Female gibbons have a single offspring every 2.5–3 years. 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 Gaoligong or Skywalker hoolock (*Hoolock tianxing*), first described in 2017 (Fan *et al.*, 2017; Fan, Turvey and Bryant, 2020). 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 south-western 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). Current estimates suggest that the population in Myanmar may be several thousands; additional surveys are needed to gather detailed data. Density estimates range from 0.76–1.0 groups/km² (Aung *et al.*, 2023).

With an estimated maximum contiguous 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, as well as hunting for food, pets, tourism and medicinal purposes. The Gaoligong hoolock is categorized as endangered on the IUCN Red List (Fan, Turvey and Bryant, 2020).

Physiology

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

The diet of the western hoolock is primarily frugivorous, supplemented with vegetative matter such as leaves, shoots, seeds, moss and flowers. While little is known about the diet of the eastern hoolock, it probably 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 thought to be territorial, although this assumption has yet to be corroborated by data. Hoolock pairs vocalize a “double solo” rather than the more common “duet” of various gibbons.



Hylobates genus

Distribution and Numbers in the Wild

Nine species are currently included in the *Hylobates* genus, although there remains some dispute about whether Abbott’s gray gibbon (*Hylobates abbottii*), the Bornean gray gibbon (*Hylobates funereus*) and Müller’s gibbon (*Hylobates muelleri*) represent full species (see Table AO2).

This genus of gibbon was and is found in discontinuous tropical and subtropical forests, from southwestern China—where the genus has been extirpated—through Indochina, the Malay Peninsula and Thailand to the islands of Borneo, Java and Sumatra (Fan, 2017; Wilson and Reeder, 2005; see Figure AO2). The least abundant species is the moloch gibbon (*Hylobates moloch*); the 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 the hybrids 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.

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 AO2). Somewhat less widely distributed than the *Hylobates* genus, the *Nomascus* genus is present in Cambodia, the 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 37 Hainan gibbons (*Nomascus hainanus*) (Fan, 2017).⁴ Population estimates for the northern and southern white-cheeked crested gibbons (*Nomascus leucogenys* and *Nomascus siki*, respectively) are available for

some sites, and overall numbers are known to be severely depleted. The northern and southern yellow-cheeked crested gibbons (*Nomascus annamensis* and *Nomascus gabriellae*, respectively) have the largest populations among the *Nomascus* gibbons.

All species are listed in CITES Appendix I. On the IUCN Red List, five are categorized as critically endangered: the Cao Vit and Hainan gibbons, the northern and southern white-cheeked crested gibbons, and the western black crested gibbon. Two are listed as endangered: the northern and southern yellow-cheeked crested gibbons (IUCN, 2022). Major threats to these populations include hunting for food, pets and medicinal purposes, as well as habitat loss and fragmentation.

► *Physiology*

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

Social Organization

Gibbons of the *Nomascus* genus are mainly socially monogamous, although 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, albeit 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 (IUCN, 2022; Nijman *et al.*, 2020).

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 the 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 give chase to neighboring males. One group's calls inhibit nearby groups and, consequently, they 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 Socioecology⁵

This section presents an overview of the socioecology of apes: bonobos; chimpanzees; eastern and western gorillas; Bornean, Sumatran and Tapanuli orangutans; and gibbons (including siamangs).

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). Gorillas live in ten African countries (Maisels, Bergl and Williamson, 2018; Plumptre, Robbins and Williamson, 2019). Orangutans are found in Asia—in both Indonesia and Malaysia—and are the only apes 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, 2019b; Think *et al.*, 2010).

Social Organization

Apes vary considerably in their social organization. While orangutans lead semi-solitary lives, some gibbons form family groups with monogamous pairs, and African great apes—bonobos, chimpanzees and gorillas—live in larger social groupings.

BOX AO1

IUCN Red List Categories and Criteria, and CITES Appendices

The International Union for Conservation of Nature (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 I. Full details of the IUCN Red List categories and criteria (in English, French, Japanese and Spanish) can be viewed and downloaded :

<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, so long as the transfers do not contravene national legislation. Such exceptional trade requires both an import permit and an export permit, or a re-export certificate—which authorities grant only if they determine that the transfers are not likely to have a

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%

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 AO2**Great Apes and Gibbons**

IUCN Red List category: ● Vulnerable ● Endangered ● Critically endangered

Great ape genus	Species	Scientific name	Range countries
Pan	Bonobo	<i>Pan paniscus</i>	■ Democratic Republic of Congo (DRC)
	Central chimpanzee	<i>Pan troglodytes troglodytes</i>	■ Angola ■ Cameroon ■ Central African Republic ■ DRC ■ Equatorial Guinea ■ Gabon ■ Republic of Congo
	Eastern chimpanzee	<i>Pan troglodytes schweinfurthii</i>	■ Burundi ■ Central African Republic ■ DRC ■ Rwanda ■ South Sudan ■ Tanzania ■ Uganda
	Nigeria–Cameroon chimpanzee	<i>Pan troglodytes ellioti</i>	■ Cameroon ■ Nigeria
	Western chimpanzee	<i>Pan troglodytes verus</i>	■ Ghana ■ Guinea ■ Guinea-Bissau ■ Ivory Coast ■ Liberia ■ Mali ■ Senegal ■ Sierra Leone
	Gorilla	Cross River gorilla	<i>Gorilla gorilla diehli</i>
Grauer's gorilla		<i>Gorilla beringei graueri</i>	■ DRC
Mountain gorilla		<i>Gorilla beringei beringei</i>	■ DRC ■ Rwanda ■ Uganda
Western lowland gorilla		<i>Gorilla gorilla gorilla</i>	■ Angola ■ Cameroon ■ Central African Republic ■ Equatorial Guinea ■ Gabon ■ Republic of Congo
Pongo	Northeast Bornean orangutan	<i>Pongo pygmaeus morio</i>	■ Indonesia ■ Malaysia
	Northwest Bornean orangutan	<i>Pongo pygmaeus pygmaeus</i>	■ Indonesia ■ Malaysia
	Southwest Bornean orangutan	<i>Pongo pygmaeus wurmbii</i>	■ Indonesia
	Sumatran orangutan	<i>Pongo abelii</i>	■ Indonesia
	Tapanuli orangutan	<i>Pongo tapanuliensis</i>	■ Indonesia

Gibbon genus	Species (excluding subspecies)	Scientific name	Range countries
Hoolock	Eastern hoolock	<i>Hoolock leuconedys</i>	■ China ■ Myanmar
	Gaoligong hoolock (a.k.a. Skywalker hoolock)	<i>Hoolock tianxing</i>	■ China ■ Myanmar
	Western hoolock	<i>Hoolock hoolock</i>	■ Bangladesh ■ India ■ Myanmar
Hylobates	Abbott's gray gibbon	<i>Hylobates abbotti</i>	■ Indonesia ■ Malaysia
	Agile gibbon (a.k.a. dark-handed gibbon)	<i>Hylobates agilis</i>	■ Indonesia ■ Malaysia
	Bornean gray gibbon (a.k.a. northern gray gibbon)	<i>Hylobates funereus</i>	■ Brunei ■ Indonesia ■ Malaysia
	Bornean white-bearded gibbon (a.k.a. Bornean agile gibbon)	<i>Hylobates albibarbis</i>	■ Indonesia
	Kloss's gibbon (a.k.a. Mentawai gibbon)	<i>Hylobates klossii</i>	■ Indonesia
	Lar gibbon (a.k.a. white-handed gibbon)	<i>Hylobates lar</i>	■ Indonesia ■ Lao People's Democratic Republic (PDR) ■ Malaysia ■ Myanmar ■ Thailand
	Moloch gibbon (a.k.a. Javan gibbon, silvery gibbon)	<i>Hylobates moloch</i>	■ Indonesia
Müller's gibbon (a.k.a. Müller's gray gibbon, southern gray gibbon)	<i>Hylobates muelleri</i>	■ Indonesia	

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, 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 10–120 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, around 8 years of age in bonobos, and between 8 and 14 in chimpanzees (Hashimoto, 1997; Walker *et al.*, 2018).

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

	Pileated gibbon (a.k.a. capped gibbon, crowned gibbon)	<i>Hylobates pileatus</i>	<ul style="list-style-type: none"> ■ Cambodia ■ Lao PDR ■ Thailand
Nomascus	Cao Vit gibbon (a.k.a. eastern black crested gibbon)	<i>Nomascus nasutus</i>	<ul style="list-style-type: none"> ■ China ■ Viet Nam
	Hainan gibbon (a.k.a. Hainan black crested gibbon, Hainan black gibbon, Hainan crested gibbon)	<i>Nomascus hainanus</i>	<ul style="list-style-type: none"> ■ China (Hainan Island)
	Northern white-cheeked crested gibbon (a.k.a. northern white-cheeked gibbon, white- cheeked gibbon)	<i>Nomascus leucogenys</i>	<ul style="list-style-type: none"> ■ Lao PDR ■ Viet Nam
	Northern yellow-cheeked crested gibbon (a.k.a. northern buffed-cheeked gibbon)	<i>Nomascus annamensis</i>	<ul style="list-style-type: none"> ■ Cambodia ■ Lao PDR ■ Viet Nam
	Southern white-cheeked crested gibbon (a.k.a. southern white-cheeked gibbon)	<i>Nomascus siki</i>	<ul style="list-style-type: none"> ■ Lao PDR ■ Viet Nam
	Southern yellow-cheeked crested gibbon (a.k.a. red- cheeked gibbon, buff-cheeked gibbon, buffy-cheeked gibbon)	<i>Nomascus gabriellae</i>	<ul style="list-style-type: none"> ■ Cambodia ■ Viet Nam
	Western black crested gibbon (a.k.a. black crested gibbon, black gibbon, concolor gibbon, Indochinese gibbon)	<i>Nomascus concolor</i>	<ul style="list-style-type: none"> ■ China ■ Lao PDR ■ Viet Nam
Symphalangus	Siamang	<i>Symphalangus syndactylus</i>	<ul style="list-style-type: none"> ■ Indonesia ■ Malaysia

Sources: IUCN (2023); Mittermeier, Rylands and Wilson (2013); author knowledge and experience; S. Wich, personal communication, 2021 and E.A. Williamson, personal communication, 2022

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. 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

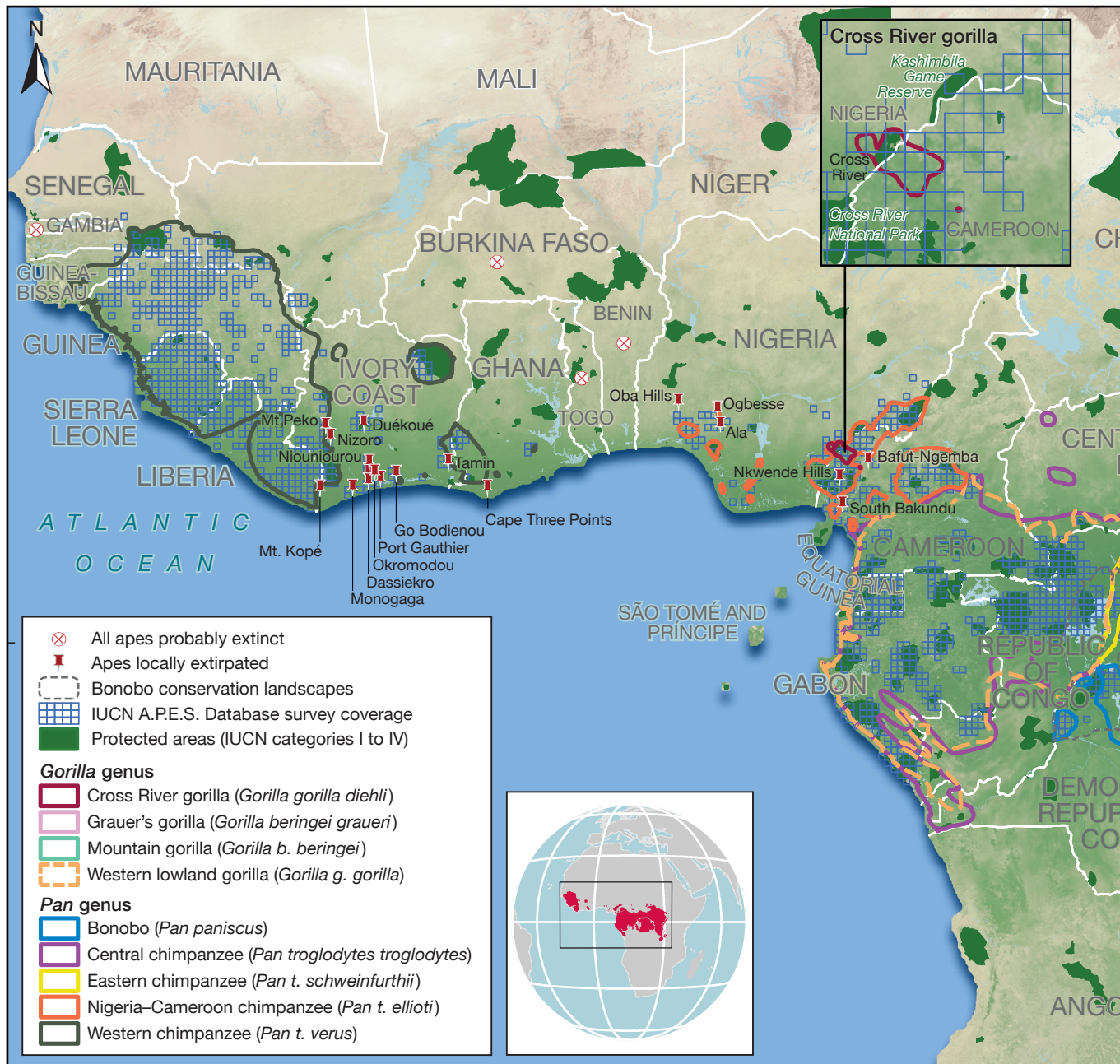
blackbacks or young silverbacks (about 13–15 years of age). Males may be solitary for several years before forming a group. Male western gorillas tend to acquire groups around age 18, a few years later than mountain gorillas, who typically become dominant around 15 years of age. Western gorilla males almost exclusively follow the path of becoming solitary and forming new groups after females join them. Mature 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, and 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 group: either they remain in the group and attempt a takeover

from within, or they emigrate to become a solitary male and eventually form new groups (Robbins and Robbins, 2018).

The three orangutan species are semi-solitary, do not exhibit territorial behavior

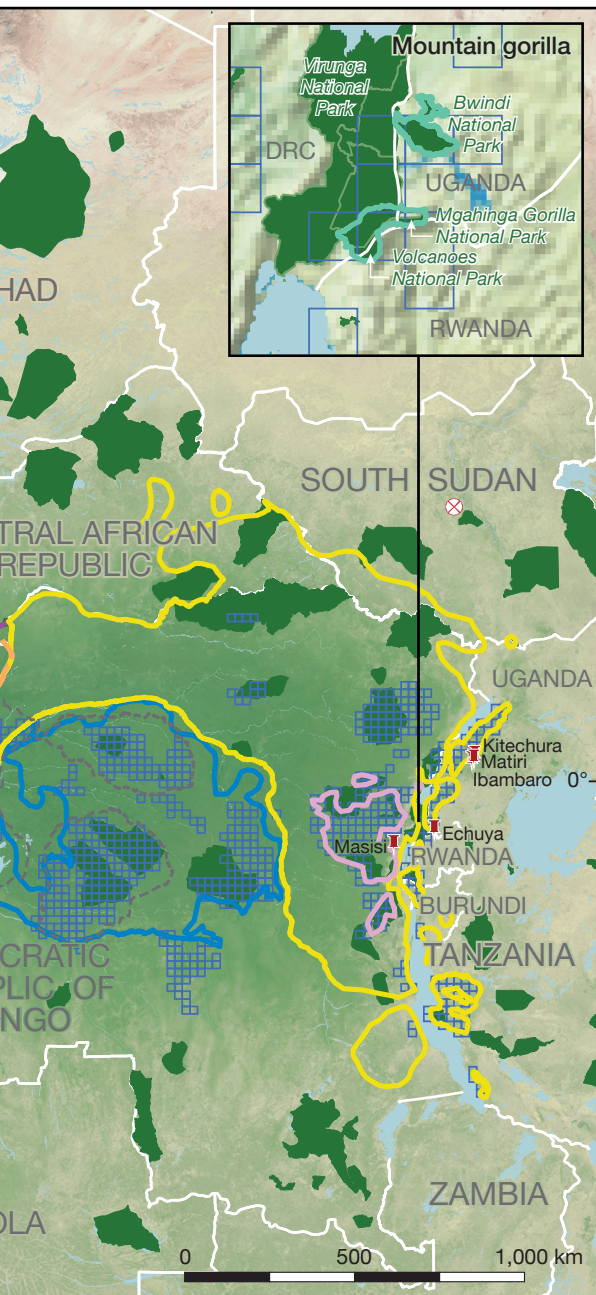
Figure AO1
Ape Distribution in Africa⁶



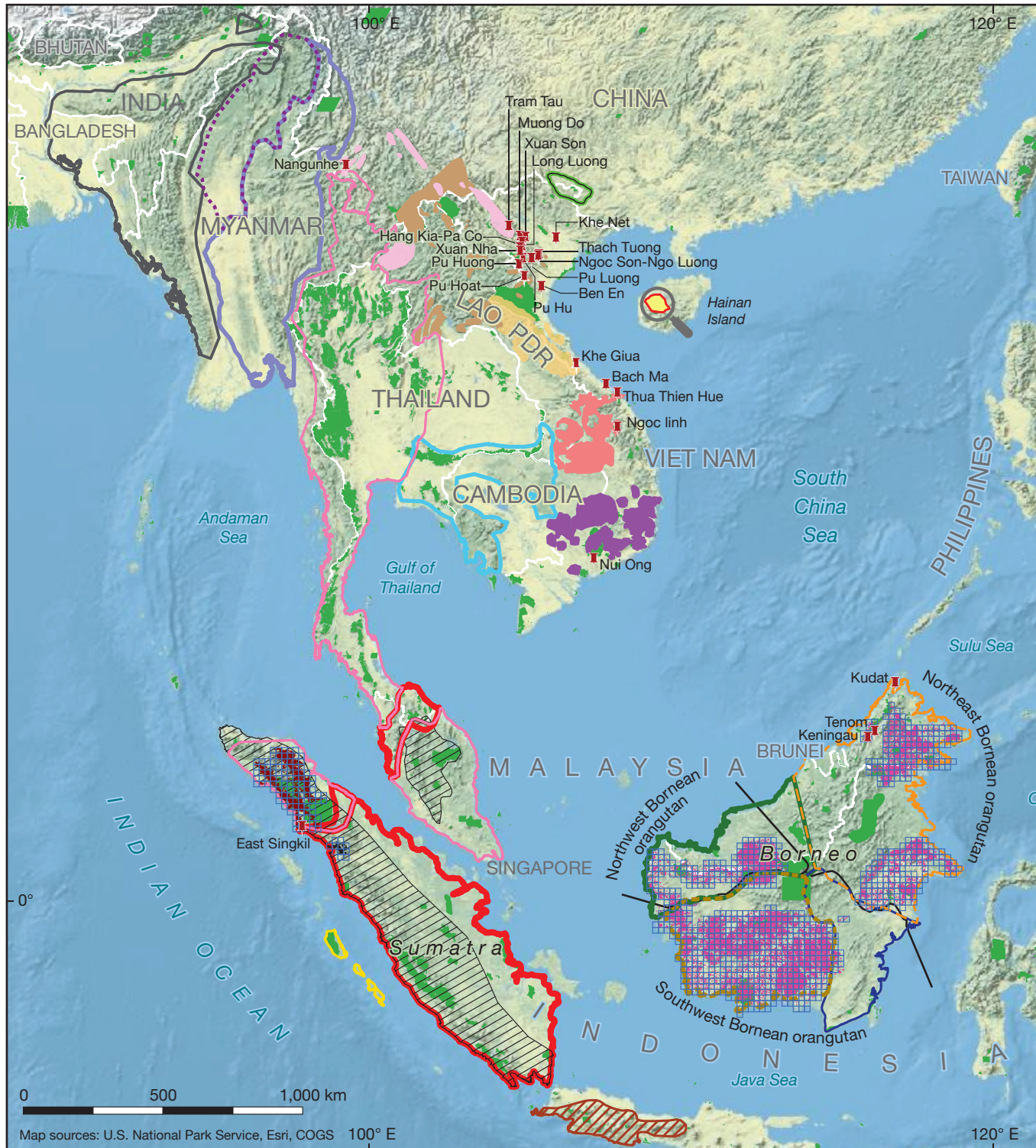
and have loosely defined communities. They are not considered “social” animals, but they exhibit an individual-based fission–fusion social organization (Roth *et al.*, 2020; van Schaik, 1999). The basic social

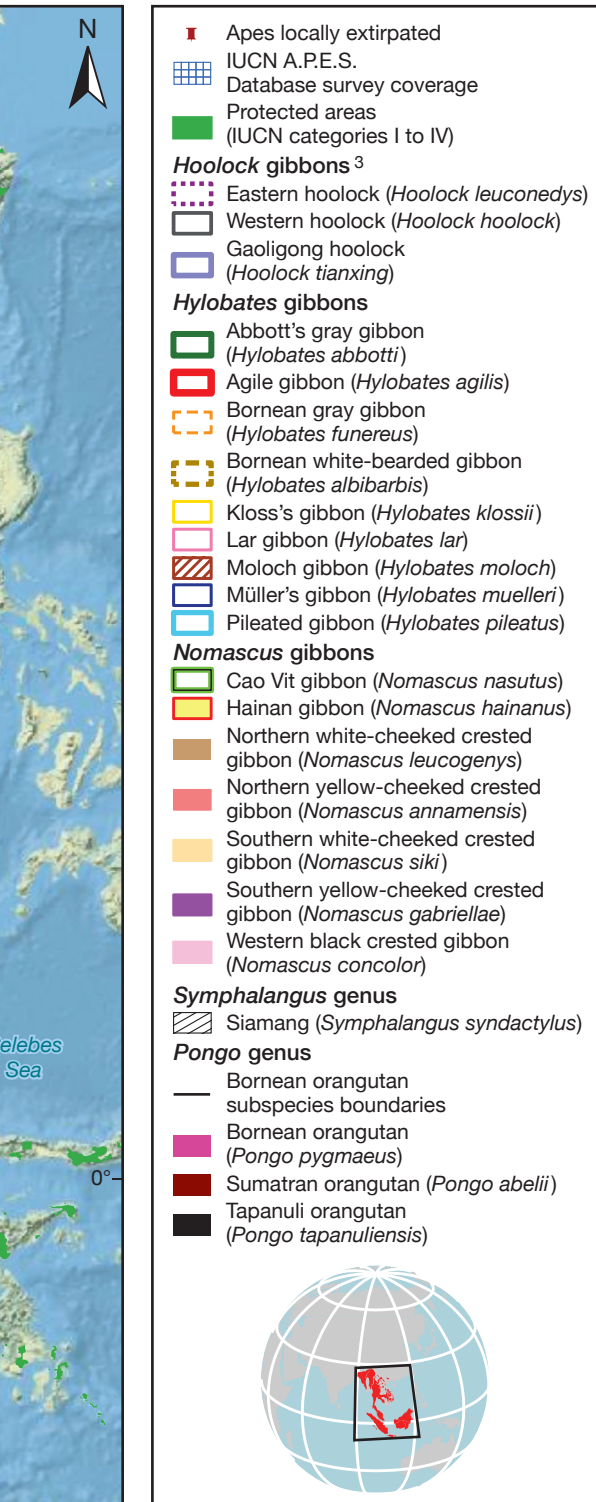
unit is a single individual, although adult females are usually found with one baby or one baby and an adolescent. Flanged adult males, characterized by fatty cheek pads and large size, lead a semi-solitary existence and are rather intolerant of other flanged males and, to a lesser degree, unflanged ones (Emery Thompson, Zhou and Knott, 2012; Spillmann *et al.*, 2017; Utami-Atmoko *et al.*, 2009). 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 (van Schaik, 1999; Wich *et al.*, 2006). Females associate more with their maternal kin; unrelated individuals show low social tolerance and sometimes exhibit aggression, which can lead to death (Knott *et al.*, 2008; Marzec *et al.*, 2016). Male orangutans are the dispersing sex: upon reaching sexual maturity, they leave the area where they were born to establish their own range (Arora *et al.*, 2012). Female orangutans show a strong natal philopatry and, upon adulthood, part of their range overlaps with their natal range (Ashbury *et al.*, 2020; van Noordwijk *et al.*, 2012). Orangutans have a polygynandrous mating system, within which males pursue a roving strategy. Although females tend to prefer flanged males for mating, unflanged males also produce a significant number of offspring in a population (Goossens *et al.*, 2006; Utami-Atmoko *et al.*, 2009).

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).



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 PSG SGA, n.d.-b).

Figure A02**Ape Distribution in Asia⁷**



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 population sizes, compression scenarios or sub-optimal 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 habitat 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 subadult gibbons to determine maximum distances over which gibbons can disperse (perhaps with the assistance of canopy bridges).

Habitat Type and Status

Most apes live in various types of closed-canopy, moist, mixed tropical forest, 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 (asl) across undulating terrain in the DRC, south of the Congo River (Fruth *et al.*, 2016; Fruth, Williamson and

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 PSG SGA, n.d.-b).

Richardson, 2013). Eastern chimpanzees and eastern gorillas can range above 2,000 m altitude. On average, Bornean orangutans prefer low-ranging areas between sea level and 500 m asl, although they can sometimes be found in forests above 500 m asl (Nowak *et al.*, 2017; Payne, 1988). In Sumatra, great apes generally live at higher elevations: the Sumatran orangutan is found from sea level to more than 1,500 m asl, and the Tapanuli orangutan is typically found above 500 m asl, but this is due to deforestation in their historic range, which included much lowland forest (Meijaard *et al.*, 2021; Wich *et al.*, 2016).

Most chimpanzees and bonobos inhabit evergreen forests, but some populations also live in deciduous woodland and drier savannah-dominated habitats interspersed with gallery forest. Although many populations are found in protected areas, a great number of chimpanzee communities occur outside. Indeed, the majority of chimpanzees in 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). In Indonesian Borneo, half of the wild orangutan population is surviving outside of protected forests, in areas that are prone to human development and transformation. In Sabah and Sarawak—the Malaysian parts of Borneo—orangutans are mostly found in protected primary and degraded forests (Ancrenaz *et al.*, 2016). The majority of Sumatran orangutans occur in primary protected forests (Nowak *et al.*, 2017; Singleton *et al.*, 2017). Several species of great apes are increasingly found in human-made mosaic landscapes dominated by agriculture and other types of land uses (Spehar *et al.*, 2018). Gibbons range from montane to

lowland peat swamp habitats from sea level to elevation of up to 2,700 m (Hu *et al.*, 2018). Many gibbons exist outside protected areas, but as they are wholly arboreal, they are unable to survive in anthropogenic mosaic landscapes (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. On the whole, 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 (Campbell-Smith *et al.*, 2011b; Seiler and Robbins, 2016). Succulent fruits are the main source of nutrition for bonobos, chimpanzees and orangutans, as well as gorillas, except at altitudes where few fleshy fruits are available. Although bonobos are mainly fruit eaters, they 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.⁸ 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; Williamson *et al.*, 1990). While gorillas incorporate a

“Great apes are adapted to a plant diet, but all taxa consume insects, and some kill and eat small mammals.”

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).

Similarly, in Asia, orangutans feed primarily on fruits, but they consume more bark and young leaves when fruit sources become scarce, adapting 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. For example, a number of tree species that had never been recorded as part as the Sumatran orangutan diet are regularly consumed by the newly described Tapanuli orangutans (Wich *et al.*, 2014b). The resilience of the species and its ability to cope with drastic habitat changes is illustrated by records of species' presence in acacia plantations in East Kalimantan; mosaics of mixed agriculture in Sumatra; agricultural landscapes dominated by oil palm plantations in Borneo; and forests exploited for timber (Ancrenaz *et al.*, 2010, 2015; Campbell-Smith *et al.*, 2011a; Meijaard *et al.*, 2010; Wich *et al.*, 2016). In these disturbed landscapes, Bornean orangutans rely more on young shoots and leaves than they do in primary forest.

Gibbons are reliant on forest ecosystems for food. Their 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, 2011; Cheyne, 2008b; 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). Gibbons have not been observed to forage on crops (either on plantations or small-scale farms), yet it is possible that they exploit disturbed areas if necessary.

“Foraging in complex forest environments requires spatial memory and mental mapping.”

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 vary dramatically in size, ranging from around 10 km² to 90 km² (1,000–9,000 ha), depending on the habitat and resource distribution. Populations in drier and more open habitats have 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.*,

“Territorial apes whose habitats are destroyed encounter great difficulties establishing a new territory nearby, where other animals are already established.”

2008). Victors benefit by gaining females or increasing the size of their range. Chimpanzees are generally highly intolerant of neighboring groups and intergroup encounters can result in lethal attacks among males in particular (Mitani, Watts and Amsler, 2010; Watts *et al.*, 2006; Wilson *et al.*, 2014b). 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).

Home ranges of bonobos also vary significantly, from 20 km² to 60 km² (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 tolerance than conflict (Lucchesi *et al.*, 2020).

Eastern gorillas range over areas measuring 6–34 km² (600–3,400 ha), and western gorilla home ranges average 10–20 km² (1,000–2,000 ha)—and potentially up to 50 km² (5,000 ha).⁹ Gorillas are not territorial; they have overlapping home ranges that they do not actively defend. There is evidence, however, 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). Gorillas preferentially use areas of their home range that have higher food availability, which means their movement patterns may vary seasonally according to fruit availability (Seiler *et al.*, 2018; Seiler and Robbins, 2020). 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).

A male orangutan's range encompasses several 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 (Spillmann *et al.*, 2017). Unflanged adult males have no strictly defined home range and move over large distances (Utami-Atmoko *et al.*, 2009). 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). Female orangutans have longer daily travel distances and larger home ranges when they are young and nulliparous—during their “exploration phase”—than during adulthood (Ashbury *et al.*, 2020). As long as distance between males is maintained, physical conflicts are rare; however, close encounters between adult males can trigger aggressive displays that sometimes lead to fights and possibly death (Knott, 1998). Females show a life-long site fidelity and live in overlapping and rather stable home ranges, but they may defend the core area of their range against female intruders, especially unrelated individuals (Ashbury *et al.*, 2020; Knott *et al.*, 2008).

Territorial apes whose habitats are destroyed encounter great difficulties establishing a new territory nearby, where other animals are already established. Indeed, in these situations the animals whose territory has been destroyed usually slowly die off.

African apes are semi-terrestrial and often rest on the ground during the daytime. In contrast, orangutans are almost exclusively arboreal, although in Borneo, they can walk on the ground for considerable distances in all types of natural and human-

made habitats (Ancrenaz *et al.*, 2014; Loken, Boer and Kasyanto, 2015; Loken, Spehar and Rayadin, 2013). Consequently, they are able to cross open, artificial infrastructure 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 (Ancrenaz *et al.*, 2021). High 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.

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 western gorillas declines with increasing availability of understory vegetation, varying between approximately 500 m and 3 km per day (Seiler and Robbins, 2020). As a result of their dietary patterns, both eastern and western gorillas 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) in size, but there is considerable variation. The more northerly *Nomascus* taxa can maintain larger territories—from about 0.13 to 1.3 km² (13–130 ha)—possibly in line with lower resource abundance at certain times of year in these more seasonal forests (Fan *et al.*, 2010). Few 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 do 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 weaned great apes build nests or beds in which they spend the night. Orangutans nest only in trees; bonobos and chimpanzees may also build daytime nests in trees or on the ground to rest; and gorillas nest primarily on the ground (Prasetyo *et al.*, 2009).

Tree nests are usually constructed 10–20 m above ground. 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, Tagg and Stewart, 2018). Great apes reuse nests on rare occasions; the frequency of reuse depends largely on the availability of sleeping site locations and material for construction (Ancrenaz, Calaque and Lackman-Ancrenaz, 2004; 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). Both chimpanzees and bonobos show tree species preferences when it comes to nesting (Fruth and Hohmann, 1996).

Reproduction

Male great apes reach sexual maturity between 8 and 18 years of age, while chimpanzees attain adulthood at 8–15 years, bonobos at 10, eastern gorillas around 12–16

“Most apes do not only feed in trees, but also rest, socialize and sleep in them, although gorillas are largely terrestrial.”

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.*, 2009). Female great apes become reproductively active between the ages of 6 and 12 years: gorillas at 6–7 years, chimpanzees at 7–8, bonobos at 9–12 and orangutans at 10–11. They tend to give birth to their first offspring between the ages of 8 and 16: gorillas at 10 (with 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 (with a median around 14.5 years) (van Noordwijk *et al.*, 2018; Williamson *et al.*, 2013).

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 (Peacock and Rogers, 1959; Stevens, 2020; van Noordwijk *et al.*, 2018). 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, 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, 2011). 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 (Knott, 2001; van Noordwijk *et al.*, 2009; Williamson *et al.*, 2013). Generally, 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 and every 7–8 years in orangutans (Emery Thompson *et al.*, 2007; Robbins *et al.*, 2009; Stoinski *et al.*, 2013; van Noordwijk *et al.*, 2018). Interbirth intervals are longer for orangutans than for African apes and gibbons, indicating higher reproductive investment from the mother and conservative growth, development and reproduction related to the hypometabolism detected in this species (Pontzer *et al.*, 2016; van Noordwijk *et al.*, 2018).

Interbirth intervals can be shortened if a member of the same species—typically an unrelated adult male—kills unweaned

“All apes have slow reproductive rates; mothers invest considerable time in a single offspring and infants are slow to develop and mature.”

offspring (Harcourt and Greenberg, 2001; Hrdy, 1979). While infanticide has not been observed in bonobos and orangutans, it can occur if a female great ape with an infant transfers to a different group. A male in the new group may kill the offspring, triggering an 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. The birth rate is lower and infant mortality is higher for western gorillas than mountain gorillas (Robbins *et al.*, 2022). 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 and Wrangham, 2013; Robbins *et al.*, 2011a).

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 15–25 years) (IUCN, 2022). 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 (van Noordwijk *et al.*, 2018; Wich *et al.*, 2009a, 2009b).

Acknowledgments

Principal authors: Annette Lanjouw,¹⁰ Helga Rainer¹¹ and Alison White¹²

Socioecology section: Marc Ancrenaz,¹³ Susan M. Cheyne,¹⁴ Tatyana Humle,¹⁵ Benjamin M. Rawson,¹⁶ Martha M. Robbins¹⁷ and Elizabeth A. Williamson¹⁸

Endnotes

- 1 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).
- 2 Bergl *et al.* (2016); Hickey *et al.* (2020); IUCN (2022); Maisels, Bergl and Williamson (2018); Plumptre *et al.* (2016b).
- 3 Davis *et al.* (2013); Gaveau *et al.* (2014); Sherman *et al.* (2020); Singleton *et al.* (2017); Wich *et al.* (2012a, 2019).
- 4 For the Cao Vit and Hainan gibbons, the updated population numbers are taken from unpublished data seen by the authors.
- 5 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.* (2009a), Williamson and Butynski (2013a, 2013b) and Williamson *et al.* (2013).
- 6 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.
- 7 See Endnote 4.
- 8 Doran-Sheehy *et al.* (2009); Ganas *et al.* (2004); Masi, Cipolletta and Robbins (2009); Robbins, Ortman and Seiler (2022); Wright *et al.* (2015); Yamagiwa and Basabose (2009).
- 9 Caillaud *et al.* (2014); Head *et al.* (2013); Robbins (2011); Seiler *et al.* (2018); Williamson and Butynski (2013a, 2013b).
- 10 Arcus Foundation (www.arcusfoundation.org).
- 11 At the time of writing: Arcus Foundation (www.arcusfoundation.org).
- 12 Arcus Foundation (www.arcusfoundation.org).
- 13 HUTAN–Kinabatangan Orang-utan Conservation Programme (www.hutan.org.my).
- 14 Borneo Nature Foundation (www.borneonaturefoundation.org).
- 15 At the time of writing: University of Kent (www.kent.ac.uk/sac). Now: Re:wild (www.rewild.org/).
- 16 World Wide Fund for Nature in Asia Pacific (asiapacific.panda.org).
- 17 Max Planck Institute for Evolutionary Anthropology (www.eva.mpg.de).
- 18 University of Stirling (www.stir.ac.uk/about/faculties/natural-sciences).