Ape Socioecology

This section presents an overview of the socioecology of the different non-human apes: bonobos; chimpanzees; eastern and western gorillas; gibbons (including sia-mangs); 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

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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 nega-

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%

tive 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

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

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).

▶ 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

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]
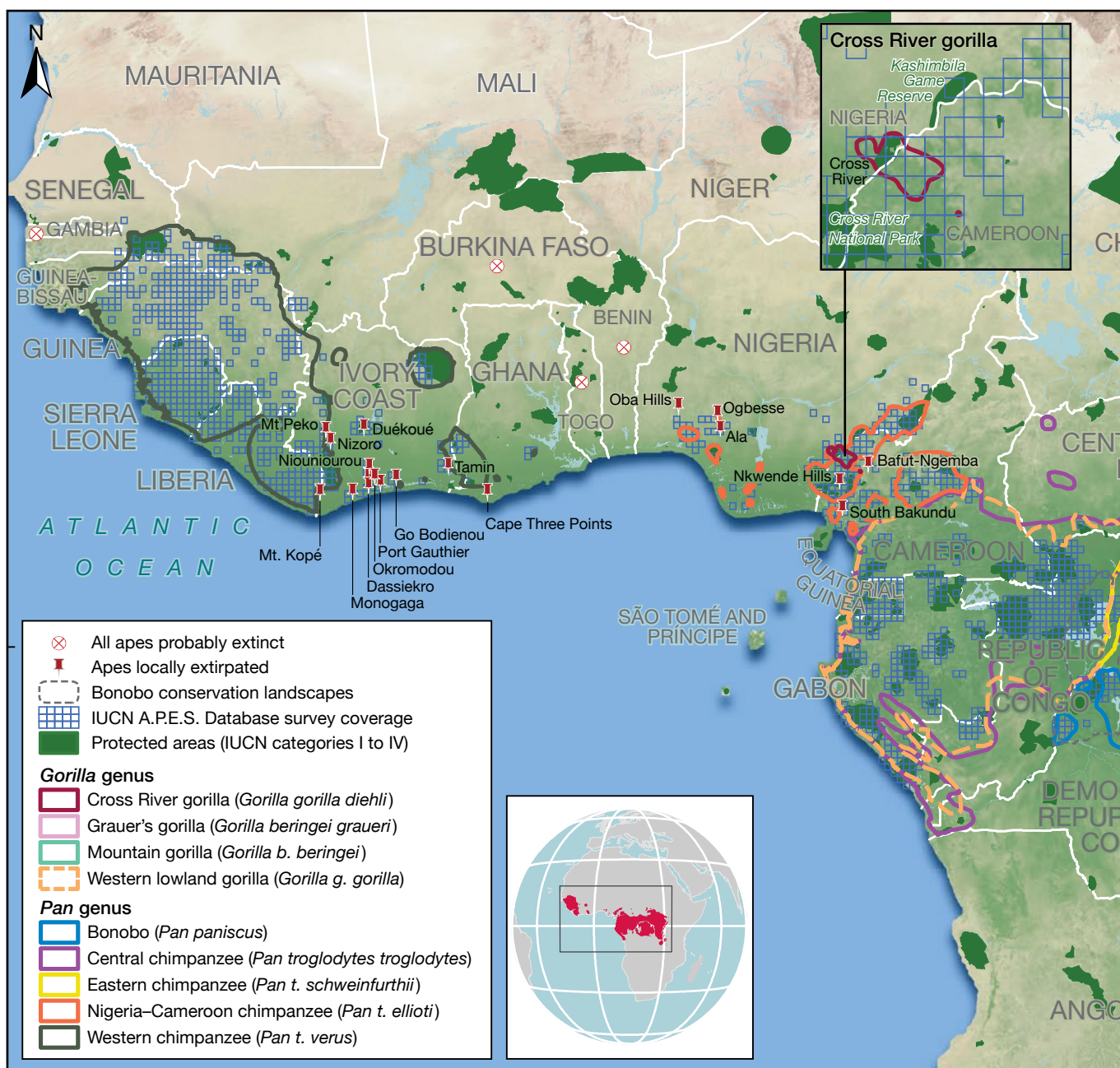
group: either they remain in the group and attempt a takeover from within, or they emigrate to become solitary males and eventually form new groups (Robbins and Robbins, 2018).
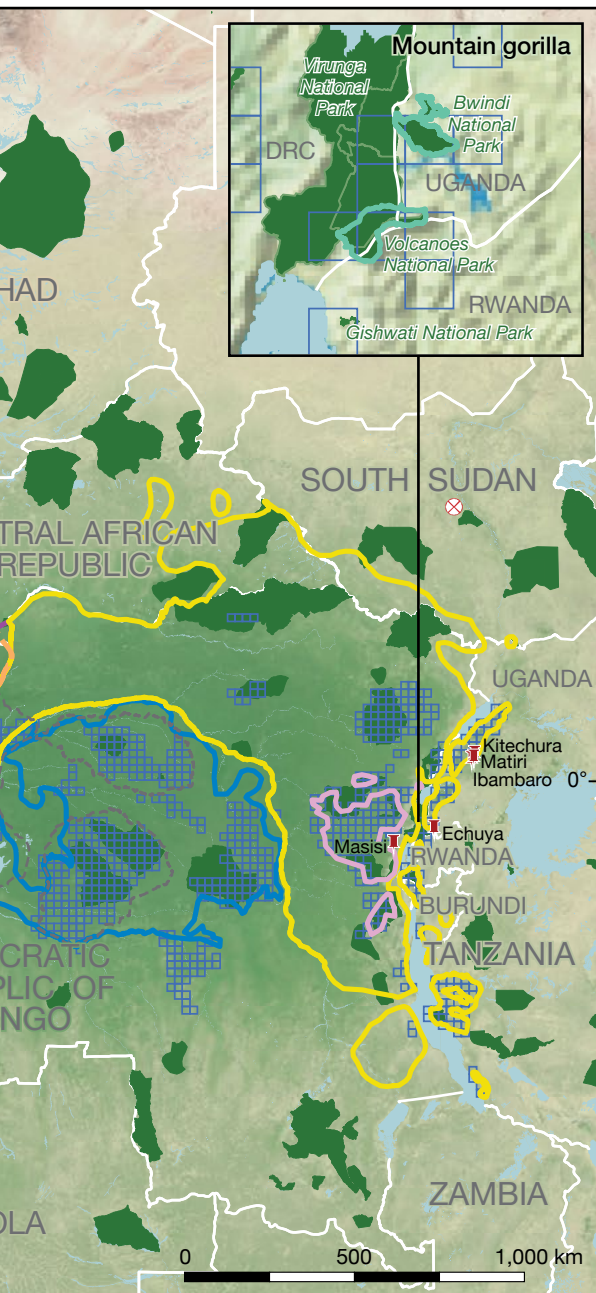
Orangutans are semi-solitary and have loosely defined communities. The basic social unit is a single individual, although adult females are usually found with one baby or one baby and an adolescent. Flanged adult males, characterized by fatty cheek pads and large size, lead a semi-solitary existence 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
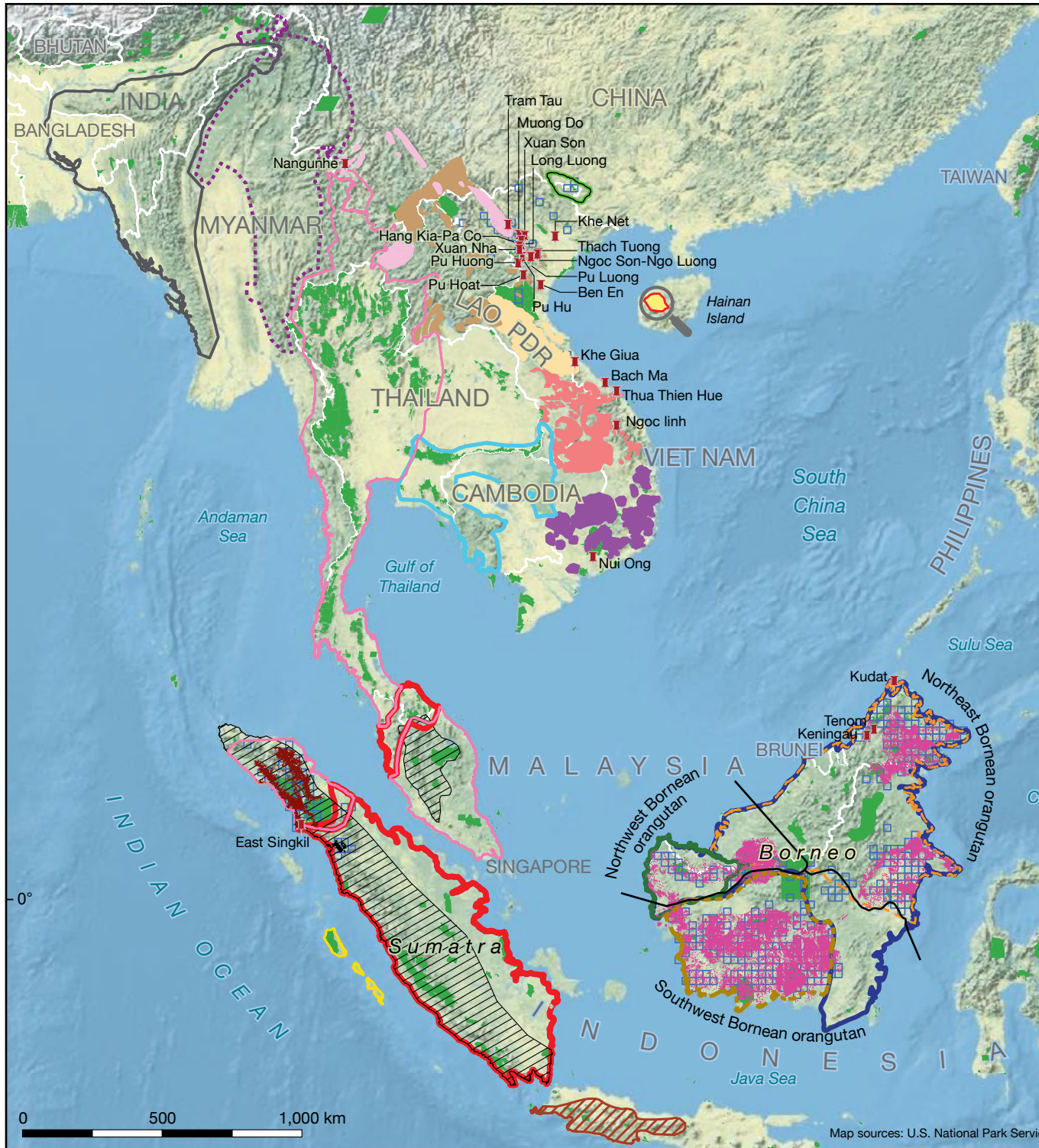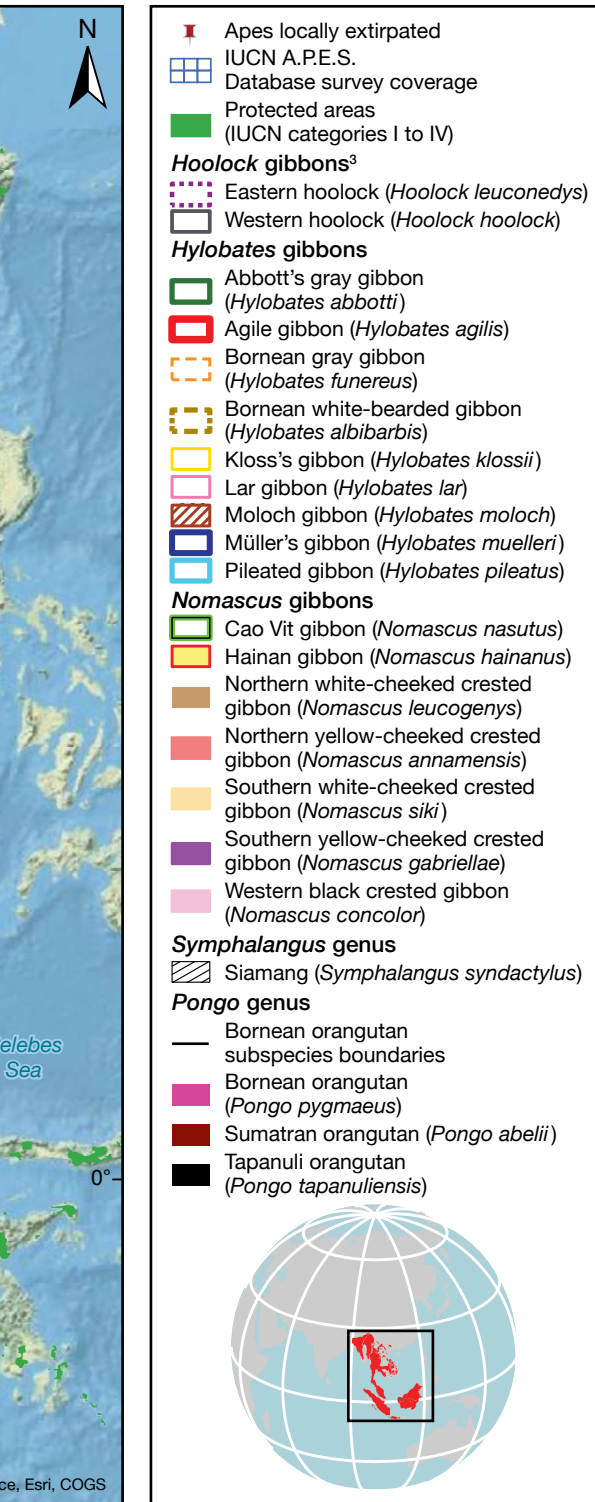
Note: Active collection of population data is ongoing for apes in various locations across their entire range. Updated information is available on the A.P.E.S. Portal (IUCN SSC, n.d.).

Figure AO2

Ape Distribution in Asia[2]

Legend (map)

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

Hoolock gibbons[3]
- ▫ Eastern hoolock (*Hoolock leuconedys*)
- ▫ Western hoolock (*Hoolock hoolock*)

Hylobates gibbons
- ▫ Abbott's gray gibbon (*Hylobates abbotti*)
- ▫ Agile gibbon (*Hylobates agilis*)
- ▫ Bornean gray gibbon (*Hylobates funereus*)
- ▫ Bornean white-bearded gibbon (*Hylobates albibarbis*)
- ▫ Kloss's gibbon (*Hylobates klossii*)
- ▫ Lar gibbon (*Hylobates lar*)
- ▨ Moloch gibbon (*Hylobates moloch*)
- ▫ Müller's gibbon (*Hylobates muelleri*)
- ▫ Pileated gibbon (*Hylobates pileatus*)

Nomascus gibbons
- ▫ Cao Vit gibbon (*Nomascus nasutus*)
- ▫ Hainan gibbon (*Nomascus hainanus*)
- ■ Northern white-cheeked crested gibbon (*Nomascus leucogenys*)
- ■ Northern yellow-cheeked crested gibbon (*Nomascus annamensis*)
- ■ Southern white-cheeked crested gibbon (*Nomascus siki*)
- ■ Southern yellow-cheeked crested gibbon (*Nomascus gabriellae*)
- ■ Western black crested gibbon (*Nomascus concolor*)

Symphalangus genus
- ▨ Siamang (*Symphalangus syndactylus*)

Pongo genus
- — Bornean orangutan subspecies boundaries
- ■ Bornean orangutan (*Pongo pygmaeus*)
- ■ Sumatran orangutan (*Pongo abelii*)
- ■ Tapanuli orangutan (*Pongo tapanuliensis*)

Celebes Sea

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ce, Esri, COGS

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.).

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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

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

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 km² (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 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 excitement rather than conflict (Hohmann et al., 1999).

Eastern gorillas range over areas of 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) (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,

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

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

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/).

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

6   Independent consultant.

7   HUTAN–Kinabatangan Orang-utan Conservation Programme (www.hutan.org.my).

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

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

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

11   Max Planck Institute for Evolutionary Anthropology (www.eva.mpg.de).

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