Ape Socioecology

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

Gorillas are the largest living primate species and the most terrestrial of all the apes. Chimpanzees are the most wide-ranging ape species in Africa, occurring across 21 countries (Oates *et al.*, 2008a). Orangutans are found in Asia—in both Indonesia and Malaysia—and are the only ape to have two distinct male types. Gibbons are the most numerous of the apes, with 19 species across Asia and Southeast Asia.

Great Ape Socioecology

Social organization differs considerably across the three great ape genera.

Both chimpanzees and bonobos form dynamic communities, fissioning into smaller parties or coming together (fusioning) according to food availability and the presence of reproductively active females (Wrangham, 1986). Chimpanzee communities average 35 members, with a known maximum of 150 members (Mitani, 2009). Bonobo communities comprise 10–120 individuals.

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

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

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BOX AO1

IUCN Red List Categories and Criteria, and CITES Appendices

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

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

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

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

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

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

Table AO1

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

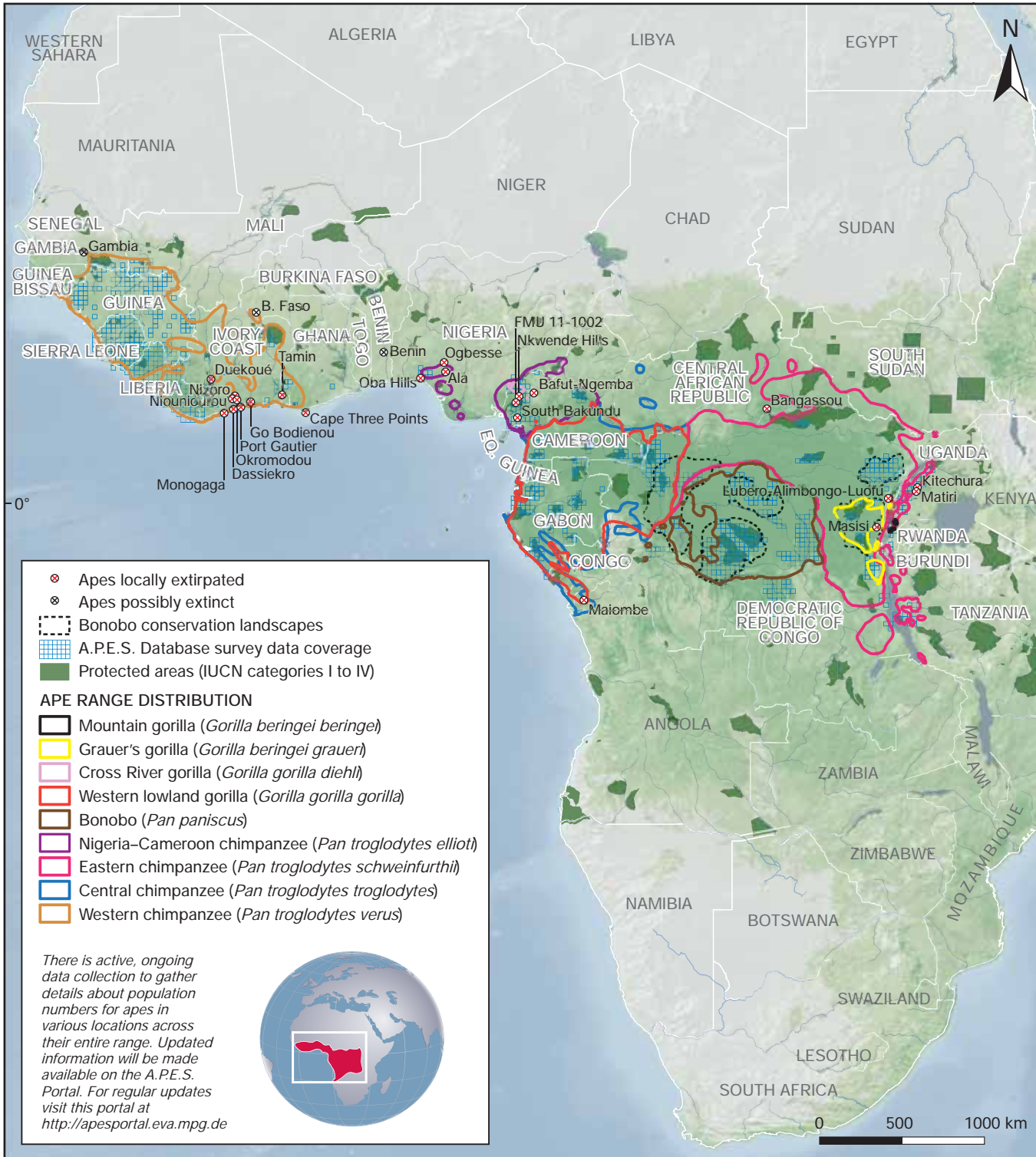| GREAT APES		
Pan genus		
Bonobo	*Pan paniscus*	■ Democratic Republic of Congo (DRC)
Central chimpanzee	*Pan troglodytes troglodytes*	■ Angola ■ Cameroon ■ Central African Republic ■ DRC ■ Equatorial Guinea ■ Gabon ■ Republic of Congo
Eastern chimpanzee	*Pan troglodytes schweinfurthii*	■ Burundi ■ Central African Republic ■ DRC ■ Rwanda ■ Sudan ■ Tanzania ■ Uganda
Nigeria–Cameroon chimpanzee	*Pan troglodytes ellioti*	■ Cameroon ■ Nigeria
Western chimpanzee	*Pan troglodytes verus*	■ Benin ■ Burkina Faso ■ Gambia ■ Ghana ■ Guinea ■ Mali ■ Senegal ■ Sierra Leone ■ Togo
Gorilla genus		
Cross River gorilla	*Gorilla gorilla diehli*	■ Cameroon ■ Nigeria
Grauer's gorilla (eastern lowland gorilla)	*Gorilla beringei graueri*	■ DRC
Mountain gorilla	*Gorilla beringei beringei*	■ DRC ■ Rwanda ■ Uganda
Western lowland gorilla	*Gorilla gorilla gorilla*	■ Angola ■ Cameroon ■ Central African Republic ■ Equatorial Guinea ■ Gabon ■ Republic of Congo
Pongo genus		
Northeast Bornean orangutan	*Pongo pygmaeus morio*	■ Indonesia ■ Malaysia
Northwest Bornean orangutan	*Pongo pygmaeus pygmaeus*	■ Indonesia ■ Malaysia
Southwest Bornean orangutan	*Pongo pygmaeus wurmbii*	■ Indonesia
Sumatran orangutan	*Pongo abelii*	■ Indonesia

►

Table AO1

Continued

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

Figure AO1

Ape Distribution in Africa

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

Ecology

Most great apes live in closed, moist, mixed tropical forest, occupying a range of forest types, including lowland, swamp, seasonally inundated, gallery, coastal, submontane, montane and secondary regrowth. Eastern and western chimpanzees also live in savannah–mosaic landscapes. The largest populations are found below 500 m elevation, in the vast swamp forests of Asia and Africa (Morrogh-Bernard *et al.*, 2003; Stokes *et al.*, 2010), although eastern chimpanzees and eastern gorillas range above 2,000 m altitude. Most chimpanzees inhabit evergreen forests, but some populations exist in deciduous woodland and drier savannah-dominated habitats interspersed with gallery forest. Although many populations inhabit protected areas, a great number of chimpanzee communities, especially on the western and eastern coasts of Africa, live outside of protected areas, including the majority of individuals in countries such as Guinea, Liberia and Sierra Leone (Kormos *et al.*, 2003; Brncic, Amarasekaran and McKenna, 2010; Tweh *et al.*, 2014).
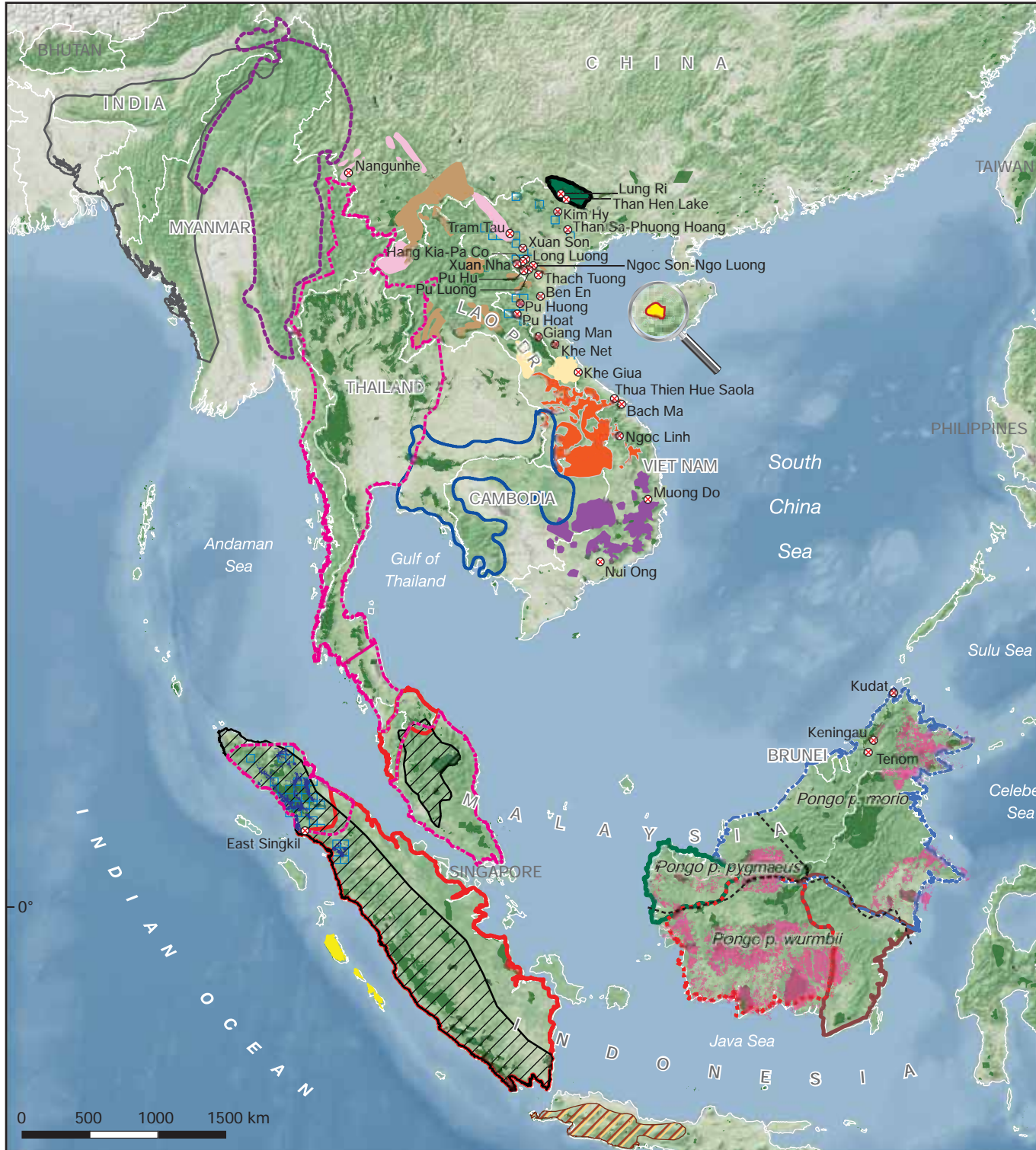
Great apes are adapted to a plant diet, but all taxa consume insects, and some kill and eat small mammals. Succulent fruits are their main source of nutrition, except at altitudes where few fleshy fruits are available (Watts, 1984). During certain periods, African apes concentrate on terrestrial herbs or woody vegetation, such as bark. Similarly, in Asia, orangutans consume more bark and young leaves when fruits are scarce. Sumatran orangutans are more frugivorous than their Bornean relatives (Russon *et al.*, 2009).
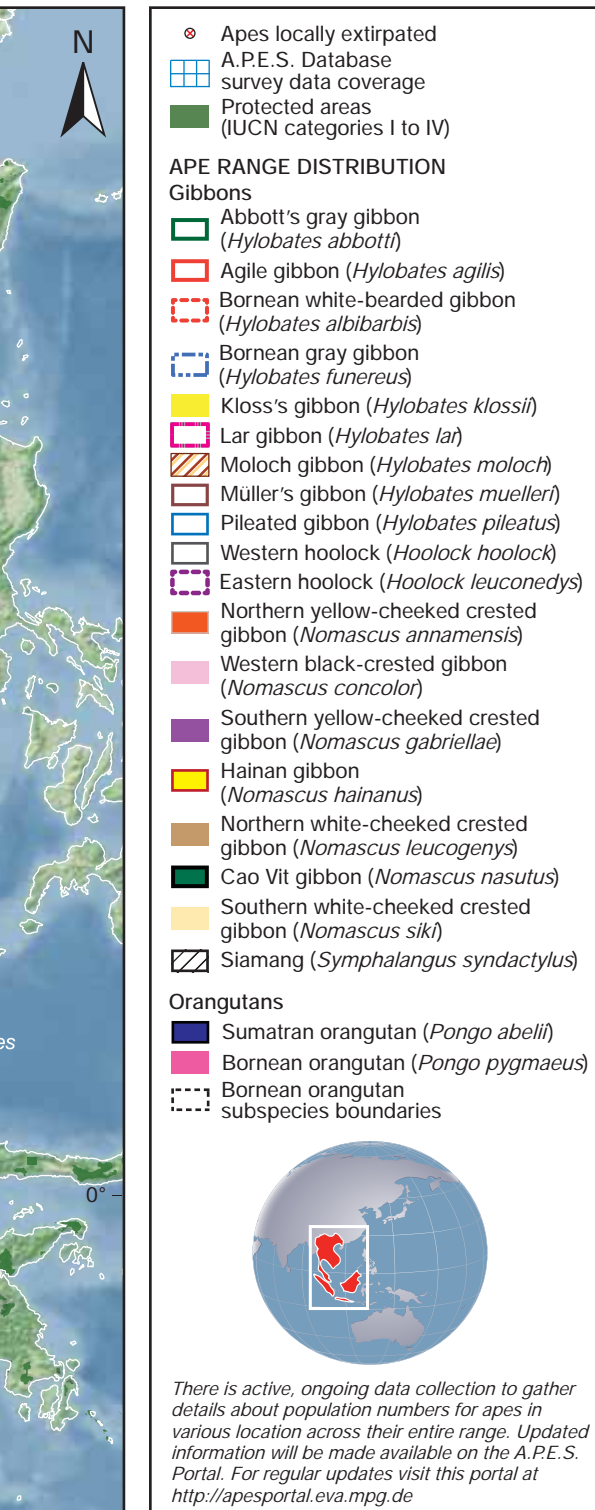
Gorillas inhabit a broad range of habitats across ten African countries. One commonality of gorillas across their range is that they rely more heavily than any other ape species on herbaceous vegetation, such as the leaves, stems and pith of understory vegetation, as well as leaves from shrubs and trees (Ganas *et al.*, 2004; Doran-Sheehy *et al.*, 2009; Masi, Cipolletta and Robbins, 2009; Yamagiwa and Basabose, 2009). Early research suggested that gorillas ate very little fruit, a finding that can be attributed to the fact that initial studies of their dietary patterns were conducted in the Virunga Volcanoes (Watts, 1984), the only habitat in which gorillas eat almost no fruit as it is virtually unavailable; these conclusions were adjusted once detailed studies were conducted on lowland gorillas. While gorillas incorporate a notable amount of fruit into their diets when it is available (Watts, 1984), they are less frugivorous than chimpanzees, preferring vegetative matter even at times of high fruit availability (Morgan and Sanz, 2006; Yamagiwa and Basabose, 2009; Head *et al.*, 2011).

The distance travelled per day by gorillas declines with increasing availability of understory vegetation, varying between approximately 500 m and 3 km per day. As a result of their dietary patterns, they are restricted to moist forest habitats (at altitudes ranging from sea level to more than 3,000 m) and are not found in savannah or gallery forests inhabited by chimpanzees.

Chimpanzees eat mainly fruit, although they present an omnivorous diet, which may include plant pith, bark, flowers, leaves and seeds, as well as fungi, honey, insects and mammal species, depending on the habitat and the community; some groups may consume as many as 200 plant species (Humle, 2011b). Chimpanzees are both terrestrial and arboreal; they live in multi-male–multi-female, fission–fusion communities. A single community will change size by fissioning into smaller parties according to resource

Figure AO2

Ape Distribution in Asia

N

Legend

⊗ Apes locally extirpated

▦ A.P.E.S. Database survey data coverage

▮ Protected areas (IUCN categories I to IV)

APE RANGE DISTRIBUTION

Gibbons

▭ Abbott's gray gibbon (*Hylobates abbotti*)

▭ Agile gibbon (*Hylobates agilis*)

▭ Bornean white-bearded gibbon (*Hylobates albibarbis*)

▭ Bornean gray gibbon (*Hylobates funereus*)

▮ Kloss's gibbon (*Hylobates klossii*)

▭ Lar gibbon (*Hylobates lar*)

▨ Moloch gibbon (*Hylobates moloch*)

▭ Müller's gibbon (*Hylobates muelleri*)

▭ Pileated gibbon (*Hylobates pileatus*)

▭ Western hoolock (*Hoolock hoolock*)

▭ Eastern hoolock (*Hoolock leuconedys*)

▮ Northern yellow-cheeked crested gibbon (*Nomascus annamensis*)

▮ Western black-crested gibbon (*Nomascus concolor*)

▮ Southern yellow-cheeked crested gibbon (*Nomascus gabriellae*)

▮ Hainan gibbon (*Nomascus hainanus*)

▮ Northern white-cheeked crested gibbon (*Nomascus leucogenys*)

▮ Cao Vit gibbon (*Nomascus nasutus*)

▮ Southern white-cheeked crested gibbon (*Nomascus siki*)

▨ Siamang (*Symphalangus syndactylus*)

Orangutans

▮ Sumatran orangutan (*Pongo abelii*)

▮ Bornean orangutan (*Pongo pygmaeus*)

▭ Bornean orangutan subspecies boundaries

0°

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

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

Great apes not only feed, but also rest, socialize and sleep in trees. Being large-brained, highly intelligent mammals, they need long periods of sleep and build nests in which they spend the night. These beds are usually constructed high in trees, 10–30 m above ground (Morgan *et al.*, 2006). African apes are semi-terrestrial and often rest on the ground during the daytime, but orangutans are almost exclusively arboreal. They are not adapted for terrestrial locomotion, although Bornean orangutans also travel on the ground in both primary and degraded habitat (Loken, Spehar and Rayadin, 2013; Ancrenaz *et al.*, 2014b). More or less restricted to the canopy, orangutans do not travel great distances on average. Bornean flanged adult males and adult females move 200 m each day, unflanged adult males usually double that distance. Sumatran orangutans move farther, but still less than 1 km each day (Singleton *et al.*, 2009). The semi-terrestrial African apes range considerably longer distances and the most frugivorous roam several kilometers each day: bonobos and western lowland gorillas average 2 km, but sometimes 5–6 km; chimpanzees travel 2–3 km, with occasional 10 km excursions. Savannah-dwelling chimpanzees generally range farther daily than their forest-dwelling counterparts. See Figure AO3.

Figure AO3

Daily Distances Travelled by Great Apes

Key

Chimpanzee = 2,000–10,000 m

Bonobo = 2,000–6,000 m

Western lowland gorilla = 2,000–6,000 m

Eastern lowland gorilla = 1,500–5,000 m

Sumatran orangutan = flanged 1,000 m, unflanged unknown

Bornean orangutan = flanged 200 m, unflanged 400 m

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

A male orangutan's range encompasses several (smaller) female ranges; high-status flanged males are able to monopolize both food and females to a degree, and so may temporarily reside in a relatively small area (4–8 km² for Bornean males). Orangutan home-range overlap is usually extensive, but flanged male orangutans establish personal space by emitting long calls (see Figure AO4). As long as distance is maintained, physical conflicts are rare; however, close encounters between adult males trigger aggressive displays that sometimes lead to fights. If an orangutan inflicts serious injury on his opponent, infection of the wounds can result in death (Knott, 1998).

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

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

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

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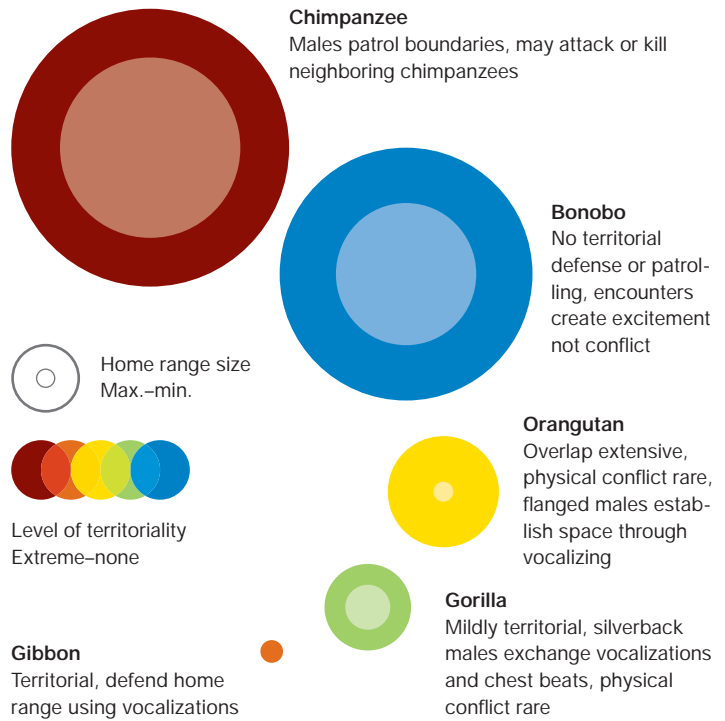
Reproduction

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

Pregnancy length in gorillas and orangutans is about the same as for humans; it is slightly shorter in chimpanzees and bonobos, at 7.5–8.0 months. Apes usually give

Figure AO4

Size of Ape Home Ranges and Levels of Territoriality

Chimpanzee
Males patrol boundaries, may attack or kill neighboring chimpanzees

Bonobo
No territorial defense or patrolling, encounters create excitement not conflict

Home range size
Max.–min.

Level of territoriality
Extreme–none

Orangutan
Overlap extensive, physical conflict rare, flanged males establish space through vocalizing

Gorilla
Mildly territorial, silverback males exchange vocalizations and chest beats, physical conflict rare

Gibbon
Territorial, defend home range using vocalizations

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

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

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

Long-term research on mountain gorillas and chimpanzees has allowed female lifetime reproductive success to be evaluated. The mean birth rate is 0.2–0.3 births/adult female/year, or one birth per adult female every 3.3–5.0 years. Mountain gorilla females produce an average of 3.6 offspring during their lifetimes (Robbins *et al.*, 2011); similarly, chimpanzees give birth to four offspring, but only 1.5–3.2 survive beyond infancy (Sugiyama and Fujita, 2011).

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

Gibbon Socioecology

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

Gibbons are reliant on forest ecosystems for food. Gibbon diets are characterized by high levels of fruit intake, dominated by figs and supplemented with young leaves, mature leaves and flowers (Bartlett, 2007; Cheyne, 2008b; Elder, 2009), although siamangs are more folivorous (Palombit, 1997). Reliance on other protein sources, such as insects, birds'

eggs and small vertebrates, is likely under-represented in the literature. The composition of the diet changes with the seasons and habitat type, with flowers and young leaves dominating during the dry season in peat-swamp forests and figs dominating in dipterocarp forests (Marshall and Leighton, 2006; Fan Peng-Fei and Jiang Xue-Long, 2008; Lappan, 2009; Cheyne, 2010). Since gibbons are important seed dispersers, their frugivorous nature is significant in maintaining forest diversity (McConkey, 2000, 2005; McConkey and Chivers, 2007).

Each family group maintains a territory that it defends from other groups. Territories average 0.42 km² (Bartlett, 2007), but there is considerable variation and some indication that the more northerly *Nomascus* taxa maintain larger territories, possibly related to lower resource abundance at some times of year in these more seasonal forests. Gibbons have been typified as forming socially monogamous family groups. Other studies, however, have revealed they are not necessarily sexually monogamous (Palombit, 1994). Notable exceptions include extra-pair copulations (mating outside of the pair bond), individuals leaving the home territory to take up residence with neighboring individuals and male care of infants (Palombit, 1994; Reichard, 1995; Lappan, 2008). Research also indicates that the more northerly *N. nasutus*, *N. concolor* and *N. haianus* commonly form polygynous groups with more than one breeding female (Zhou *et al.*, 2008; Fan Peng-Fei and Jiang Xue-Long, 2010; Fan Peng-Fei *et al.*, 2010). There is no conclusive argument regarding these variable social and mating structures; they may be natural or a by-product of small population sizes, compression scenarios or sub-optimal habitats.

Both males and females disperse from their natal groups (Leighton, 1987) and establish their own territories; females have their first offspring at around 9 years of age. Data from captivity suggest that gibbons become sexually mature as early as 5.5 years of age (Geissmann, 1991). Interbirth intervals are in the range of 2–4 years, with 7 months' gestation (Bartlett, 2007). Although captive individuals have lived upwards of 40 years, gibbon longevity in the wild is unknown but thought to be considerably shorter. Due to the gibbons' relatively late age of maturation and long interbirth intervals, reproductive lifetime may be only 10–20 years (Palombit, 1992). Population replacement in gibbons is therefore relatively slow.

Acknowledgments