

Module # 5 – Component # 2



Gorillas

Subfamily Gorillinae

Gorilla gorilla, Western gorilla
G. berengei, Eastern gorilla

When the *Guide* account was written, only one species with 2 or 3 subspecies was recognized. Current classifications followed here treat the subspecies as full species. Unless otherwise indicated, the following account applies to both species.

TRAITS

The largest primate: males 140 - 185cm (standing height) and c. 160kg (210 kg, 462 lb., is the record for a wild gorilla); females up to 150cm and 68-114 kg. Robust build with long, muscular arms and short legs, broad hands and feet with thick digits; pot belly; massive head crowned in male with conical mass of bony ridge and muscles, features (especially the shape and wrinkles of the nose) individually distinct; robust teeth (adapted for fibrous diet) and sharp canines (adult males only).

Coat: long and silky in mountain populations, shorter and sparser in lowland forms.

Colouration: blue-black to brownish-gray, naked areas (nose, lips, ears, chest, palms, soles) black, mature males with a conspicuous saddle of gray or silver hair.

Glands: armpits with 4 -7 layers of large apocrine glands in adult male which emit pungent odor under stress; apocrine and eccrine glands lubricate palms and soles

DISTRIBUTION

At some time in the past gorillas probably ranged across the rain forest north of the Congo-Ubangui-Uele river system from the Atlantic Coast to the Western Rift Valley of Central Africa. But during dry (interpluvial) periods of the Ice Age the rain forest shrank, wiping out intermediate populations and leaving western and eastern populations separated by over 1000 km. The latest classifications distinguish 2 different species and 4-5 subspecies.

G. g. gorilla, the western lowland gorilla, which inhabits the lowland rain forest. The smallest race (males 140 kg, females 75 kg) with the smallest social groups, it has relatively small jaws and teeth but a broad face, short coat often with a brownish tinge, and distinctive red forehead; mature males have a nearly white, very striking saddle.

G. b. beringei, the mountain gorilla of the Virunga volcanoes that divide DRC from Rwanda and Uganda. The best known, hairiest race, black coat turning gray with age, with very broad face and massive jaws/teeth; males average 160 kg and females 90 kg.

G. b. graueri, the eastern lowland or Grauer's gorilla, which may be the largest race (males 165 kg and 175 cm [5 ft. 8 in.] tall). With short, black fur and a narrower face than the other 2 races, this subspecies survives in isolated pockets of rain forest in eastern DR Congo and in some adjacent highland areas near the Rwanda/DR Congo border.

Of an estimated world population of 125,000 gorillas at the end of the 20th century, 98% live in Lowland Rain Forest, many of them in isolated and semi-isolated population units (none of more than 2700 animals). Some 2/3 of the Western gorillas live in Gabon and the DR Congo, which have the lowest human population density and largest surviving blocks of unlogged forest. The populations of 4,000 the eastern lowland gorillas gorilla **totalled** c. 10,000 – but that was before the civil war that has brought devastation to the DR Congo protected area. The surviving ± 450 mountain gorillas in Rwanda and Uganda, remain endangered but are presently holding their own.

ECOLOGY

Although most gorillas inhabit the warm, humid equatorial rain forest, this largely terrestrial browsing ape is concentrated in places where enough light penetrates the forest canopy to support a luxuriant understory of woody and herbaceous plants. For such a large, group-living animal, scattered small patches of forage created by single falling trees would not suffice. Waterways are lined by extensive if narrow belts of undergrowth, but forests that have been logged and cultivated are far more extensive and productive, and gorillas show a preference for regenerating secondary forest throughout their range. Thus human inroads into the primary rain forest actually enlarge the area of good gorilla habitat, so that in theory lowland gorillas should be increasing their range and numbers. Unfortunately though, large-scale logging operations expose gorillas to the commercial bushmeat trade.

Mountain gorillas inhabit montane forests between 2800 and 3400 m in the Virunga Range, and sometimes venture to 4000 m in the Afro-Alpine meadows, where, however, there is little suitable forage. Night temperatures often go below freezing, and clouds and mist obscure the sun for part or all of each day. The trees are wreathed with moss, lichens, ferns, orchids, and other epiphytes characteristic of montane cloud forest.

In the nearby Kahuzi-Biega N.P. northwest of Lake Kivu, eastern lowland gorillas live below the alpine-bamboo zone between 2000 and 2500 m; here the montane forest is dense and composed of about 26 different trees, many over 30 m tall. Mountain gorillas live above the bamboo zone, mainly on the slopes of the volcanic peaks and on the nearly level saddles between peaks in a parkland dominated by only 2 species of trees: the massive but not particularly tall *Hagenia abyssinica* (20 m) and *Hypericum lanceolatum*, which becomes dominant at higher elevations. The tree canopy shades at most 50% of the ground, which is otherwise choked with herbaceous plants up to 2 m high and tangled in vines. Here gorillas seldom need climb trees or range far to eat their fill. However the plants are inferior in variety and nutritional value to rain forest vegetation, and, apparently to compensate for the lack of certain vitamins and minerals (B₁₂, calcium, potassium), gorillas eat some animal food (invertebrates), their own dung, and mineral-rich soil.

DIET

Gorillas of Rwanda's Parc de Volcans utilize altogether some 58 different plants, of which leaves, shoots, and stems account for about 86% and fruits only 2%. Roots, bark, grubs, snails, dirt, and dung make up the balance. Just 9 different species account for 80% of the feeding records, and only 3 make up 60%. Galium, a scraggly but extremely abundant vine, made up 24% - 30% of feeding records for 3 different gorilla groups, a thistle (*Carduus afromontanus*) made up 10.5 % - 37%, and a kind of celery (*Cynoglossum*) 8.5 % - 20%. Three species of stinging nettles, a small tree (*Vernonia*), and 2 kinds of blackberries (*Rubus* species) together amounted to 8.5 % - 20% of the feeding records (Fossey and Harcourt 1977).

Seven distinct vegetation zones occur in the 25 km² study area, and the gorillas visit all of them at times when favorite foods are available in abundance. In Equatorial Guinea (Rio Muni), gorillas may subsist very largely on the profuse growths of wild ginger (*Aframomum*) which invade old clearings. They eat the leaves, pith, roots, and also the fruits, which germinate only after passing through an animal's digestive tract .

By destroying seedling trees, disturbing the soil, and generally slowing the succession back to forest, gorillas in effect cultivate and propagate their own food supply (cf. vervet Diet). Their diet is so rich in succulent herbs that they rarely need to drink.

SOCIAL ORGANIZATION:

1-male harems, non-territorial, females transfer and male offspring usually emigrate.

Writing about the reactions of people when brought face-to-face with gorillas, one primatologist aptly describes the "mingled esteem, awe and horror with which the human primate views the biggest species in the order". These feelings are inspired first and foremost by the adult male, which, it appears, has much the same effect on other gorillas. He is huge and powerful compared to them, too. Many men are bigger than a female gorilla, but a silverback male not only weighs 23 - 45 kg (50 -100 lb.) more but is about 10 times stronger than the biggest football players and wrestlers. To be armed, in addition, with big, sharp canines seems *de trop*. Small wonder, then, that all the members of a group are ever-ready to defer to their silverback; a direct look, a frown, or a grunt is usually sufficient to curb insubordination. He leads, deciding when and where his group will forage, rest, and sleep, takes precedence in any situation where only 1 animal at a time can gain access to a resource (fruiting tree, salt lick), and arbitrates disputes between his wives.

He also defends them and his children against other silverback males and against human predators – the only kind gorillas fear. And this benevolent despot also demonstrates solicitude for his family by slowing the group's pace when a member is incapacitated by injury (bite or wire-snare wound), illness, or infirmity .

A gorilla group contains from 2 to 20 animals; the largest recorded group numbered 37. The median number is 9 for eastern gorillas (6 for the Virunga population, 11 for other mountain and eastern lowland populations) and 5 (2 – 12) for western gorillas of Equatorial Guinea. The typical (median) gorilla group consists of 1 fully mature, silverback male, 1 young adult (8 - 12 years) blackback male (average weight 115 kg), 3 adult females, and 2 - 3 young (< 8 years). The maximum number of gorillas in these sex and age classes counted in a group (all in eastern populations but not of course at the same time and place) was 4 silverbacks, 5 blackbacks, 12 adult females, and 16 young. The smaller groups of western lowland gorilla may reflect the general tendency for social units to be smaller in more closed habitats, and/or dietary differences.

Female Transfer

Like the chimpanzee, red colobus, and hamadryas and gelada baboons, female gorillas normally transfer to another breeding unit before reproducing, usually when they become adolescent at about 8 years. Judging from known transfers in the Parc de Volcans, most females change groups again at least once after their initial transfer, and may end up migrating well beyond the ranges of their parent groups. In a sample of 13 females that transferred more than once, the interval between transfers averaged 3 months but varied from only 3 days to nearly 3 ½ years. As a rule, females become permanent members of the group in which they

first reproduce, for as long as their consort remains in command (cf. plains zebra).

Females sometimes join a large, long-established group, but more often they join a lone silverback or a newly established group. Female rank follows the order in which they are recruited into the harem, so it is preferable to be number 1 or number 2 rather than a later arrival. High rank entitles a female and her offspring to remain close to the harem master, where they are safest from predation and potential abductors, which may be infanticidal (see below).

Lacking kinship ties to counterbalance competition for the position of dominant female, females reserve their affiliative behaviour for their own offspring and the silverback male, with whom each maintains conjugal bonds. They may squabble over the privilege of grooming him, and rarely groom one another. Infant and juvenile offspring receive the most grooming, whether they like it or not. The silverback is thus the only common link binding together the different female matriline. Groups left leaderless by their silverback's death tend to disintegrate, as may a group that has lost all its adult females.

The members of the same matriline often bear an obvious family resemblance, notably in their "nose prints": the shape of the nostrils and the pattern of creases, which are as unique as fingerprints.

One long-studied family was distinguished by wall-eyes, another by webbed fingers and toes, both signs of inbreeding.

Male Emigration

Male offspring also emigrate during their subadult and young-adult years, starting at c. age 11. Occasionally a male remains in his father's group and, should the patriarch be aged, may eventually inherit it. But a maturing male is only likely to stick around if he has opportunities to mate with group females. Normally the harem master monopolizes all breeding; and in the event of the patriarch's death, his heir apparent is likely to be overthrown by an older, more experienced silverback.

Males cannot, of course, transfer to another group in the manner of females. Even an orphaned juvenile male that was introduced to a group that had lost all its adult females was abused by the alpha male, although the subadults and juveniles welcomed him. An orphaned juvenile female, however, was immediately accepted by a silverback with a harem. The process of emigrating and acquiring a harem normally takes years. First the young silverback becomes peripheral to his group, staying within a 300 m radius for up to 9 months before going farther away and becoming a solitary male. How soon and to what degree a male becomes peripheral depends on his relationship with his father.

Four young silverbacks that were observed for 2 to 5 years after emigrating all spent most of the time alone. Males are rarely mature and experienced enough to begin their own harems before the age of 15. To be a successful leader and

defender of females and young, a male needs to have an established home range and the self-assurance to discourage other males from invading his group. In any case, vigorous males keep trying to acquire new females.

Home Range

Yearly home ranges vary in size from 4 - 8 km² in the Virunga range to 20 - 25 km² in the lowlands. Ranges shift from year to year and the area used over a number of years may be twice as large as the yearly range. In Kahuzi-Biega N.P., 2 groups that were regularly contacted between 1966 and 1973 even exchanged home ranges. The areas patrolled by lone silverbacks are as large as those of groups. Despite extensive overlap, each unit tends to have an exclusive core area and groups go out of their way to avoid one another except when deliberately seeking a confrontation. Lone silverbacks and even established groups often explore outside their normal range and may even get lost in unfamiliar areas. In this way gorillas discover new feeding grounds and extend their range into areas where there is less competition from other groups.

Intergroup Encounters

Gorillas appear to be far more placid and inactive than chimpanzees, wandering at leisure through the undergrowth in cohesive groups while gathering and munching their vegetable food, grunting quietly, belching, and passing wind. Females and young cluster around their gentle-giant leader during rest periods, the grown-ups grooming and socializing while the youngsters play before bedding down for a midday snooze. But this picture of domestic tranquility is rudely shattered when another silverback approaches to challenge the harem master. His strength, stamina, resolve, and judgment may be tested at any time by rivals seeking to start or enlarge their own harems. The ensuing aggressive interaction, which may continue intermittently over a period of days and involve adult females as well as all the adult and subadult males, demonstrates the really ferocious competition for female gorillas.

As males continue to put on weight and muscle after maturing and gain competence with age, seniority is an advantage. But inevitably males pass their prime (few survive beyond the age of 35) and are eventually unable to withstand challenges from more vigorous rivals.

Most transfers occur during or following encounters, and most encounters occur when a group includes a female in oestrous. Of 26 females that were known to transfer over a period of 13 years, a total of 43 times, 30 transfers by 17 females took place during exciting or violent interactions between groups. In only 3 of over 20 potential transfer situations that were observed did the resident male actively prevent a female from approaching a rival silverback. Instead, harem masters seek to discourage rivals from approaching through spectacular displays of aggression featuring loud *hooting*, *chest-beating*, *display runs* through the undergrowth, slapping the ground, and *strutting* (see under Visual and Vocal

Communication). Displaying males also give off a powerful odor from their armpits detectable by humans 25 m away.

Apart from serving to discourage encounters between social units, no doubt such displays are also intended to impress females with a male's vigor and general fitness. A questing silverback, after seeking and finding a group containing a sexually receptive female, may only need to make himself seen and heard from a safe distance to entice a maiden into joining him. Since harem males generally take little interest in their immature daughters, and there is almost no evidence of abduction or coercion by suitors, one could imagine that transfers would involve little more than some noisy but harmless demonstrations of machismo.

The incidence of violence is therefore puzzling. In a sample of 64 skeletons collected in the Parc de Volcans, 74% of those belonging to mature males showed signs of healed head wounds, and 80% had broken or missing canines. An estimated 62% of all wounds suffered by females and males of the Virunga Range resulted from interactions between distinct social units. Females are most likely to suffer injury in defense of their young, when for instance a bold intruder charges into the middle of a group.

It is not uncommon for silverbacks to kill the infants of other males if they get the chance, which has the effect of speeding the mother's return to breeding condition. For instance, a lone silverback killed a 10-month baby in a fracas from which the resident male and 3 females all emerged with severe wounds. Within a few days the mother's behaviour changed. Instead of pining, she became more social and playful, a change also noted in other females after infanticide. Two months later she and an 8-year-old adolescent female transferred to a group consisting of an adult and subadult males.

ACTIVITY

Gorillas spend approximately 30% of the day feeding, 30% traveling or moving and feeding, and 40% resting. The activities of group members are closely synchronized. Peaks of feeding and movement occur within the first 3 - 4 hours of the day, after which members of a group settle down for an extended rest, followed by another feeding session beginning by 15h00. However, one group of mountain gorillas did not have marked midday rest periods and other groups may skip their rest periods occasionally. Both lowland and mountain populations arise during the first hour and retire in the last hour of daylight. On clear days, groups often linger near their beds to warm in the sun. Mountain gorillas increase rest periods to prolong basking, and on cold, misty days they may huddle motionless for long intervals.

Nests

Nine out of 10 gorillas build nests in which to sleep at night and most also make nests for their daytime siesta. The presence of suitable and adequate nesting material primarily determines the location of bedding grounds, and nests tend to

be clustered, usually in an area of less than 1/4ha). Sitting or standing, the animal reaches out and pulls, breaks, or bends-in branches, vines, or herbage which it places around and under its body to form a crude platform or hollow with a roughly circular rim. The materials, time, and effort that go into nest building all vary, as does the product, but construction takes no more than 5 minutes. There is no particular sequence in the placement of vegetation, nor any elaborate manipulation such as interlacing or weaving together of branches. In building a ground nest, the main effort goes into forming a rim, rather than padding between the gorilla and the ground. Tree nests are usually built in forks, in crotches, or along horizontal branches, and more emphasis is placed on making a strong bottom, resulting in a platform with little or no cup. A sturdy nest enables a gorilla to sleep lying down in a tree or on a steep slope, without falling. But why construct nests on flat ground? The habit may be a holdover from arboreal ancestors (see family introduction). Adult males rarely trust their bulk to a tree nest.

Gorilla groups can be accurately censused and the ages of the members deduced by the size of their nests and the dung they contain. According to some accounts, lowland gorillas rarely foul their own nests, whereas mountain gorillas regularly defecate and sleep on their dung.

However, the 3-lobed boluses have the fibrous consistency and smell of horse manure and do not soil their coats like the messier feces of frugivorous primates. Infant gorillas sleep in their mothers' nests until the age of 3 or until the birth of a sibling, although individuals as young as 8 months practice nest building.

FORAGING AND DAY-RANGING

How far gorillas travel in a day varies between areas, between seasons, and between and within groups, depending on the temporal and seasonal distribution of food plants, and also – since different groups avoid one another – on the ranging patterns of other gorillas. Daily journeys vary between 100 and 2500 m, averaging 350 - 530 m for Virunga groups, and about a kilometer in Kahuzi-Biega N.P. and in Equatorial Guinea.

Gorillas that enter high forest are surprisingly arboreal compared to the Virunga population. To get delicacies such as "mistletoe" (*Loranthus*) and the fruits of *Syzygium* or *Myrianthus* trees, juveniles readily climb 40 m to reach the upper canopy; one blackback ascended to 35 m and a 200 kg silverback climbed as high as 20 m.

Gorillas feeding in trees assume every possible position from seated to hanging nearly upside down by their feet. On the ground they usually sit and reach out in all directions to gather edible plants (one advantage of long arms). After consuming most of the forage within easy reach, the gorilla moves a few steps, grabs a handful of food, and sits down to resume eating. In general, gorillas show great skill and dexterity in exposing and eating the palatable portions of each plant, whether it be the roots, fruits, shoots, leaves,

bark, pith, or the grubs concealed in rotting wood. But they have not been seen to prepare and use tools (cf. chimpanzee).

Gorillas very rarely compete over or share food. Adults tend to maintain a much wider spacing (10 to >20 m) while feeding than while resting, and a foraging group may be spread as wide as 100 m. However, sometimes they cluster around certain plants: for example, a wild banana tree that was fed upon until it had been almost totally demolished. Whenever access is limited, the alpha male may pull rank.

SOCIAL BEHAVIOUR: COMMUNICATION

Vocal Communication

Somewhere around 92% of the vocalizations emitted by gorillas are produced by adult males, an indication of how completely harem males rule the roost. Females emit a mere 4% of the vocalizations, infants 3%, and juveniles less than 1 %. The common calls are summarized below.

Male Loud Calls:

1. Roar. A low-pitched, abrupt outburst of sound, forced out through open mouth, produced only by silverbacks and large blackbacks. Roars of high intensity are "probably among the most explosive sounds in nature" (Schaller 1963, p.218). Context: given only in situations of stress or threat, primarily in response to disturbance by humans. Roars may be individually recognizable and are almost invariably followed by aggressive displays, ranging from bluff charges to short lunges.

Response: group seeks protection behind silverback.

2. Wraagh. Another explosive, monosyllabic outburst but not as deep as a roar and less shrill than a scream (no. 4 below). Individual differences were noted in the frequency concentrations of these calls, which are more harmonically structured than roars. Although all adult gorillas can produce the call, over 9 out of 10 are emitted by silverbacks, in response to sudden stress, such as the unexpected arrival of a human, alarm calls of other species, thunderclaps, wind gusts, and other startling noises. Unlike no. 1, this call is never accompanied by aggressive displays, but expresses alarm and group members respond by scattering.

3. Hoot series. Far-carrying (up to 2 km), low-pitched but clear and distinct *hoo-hoo-hoos* repeated 2 - 20 or more times to a series, usually as a prelude to *chest-beating* (see below). A male advertising call which functions to maintain intergroup spacing, a *hoot series* builds up in volume, the hoots becoming longer and plaintive sounding toward the end; the lengthier the series, the more individualistic are the fluctuations in harmony and phasing. The mouth is parted and the lips pursed. Other associated behaviours are discussed under *chest-beating*. The call is usually given in response to the sight or sound of non-group members. When given without other, non-vocal sounds, hoots do not reveal the

precise location of the caller, making this call suitable for vocal probing (e.g., to determine whether other silverbacks are in the area while minimizing the risk of a confrontation).

Other Alarm Calls:

4. Scream. Extremely loud, shrill, and prolonged (up to 2 seconds) sounds repeated up to 10 times. Screams may be given by all classes when a group is upset, say, by an encounter with humans, but is particularly associated with quarreling between group members.

5. Question bark. A short call of 3 notes with the first and third lower than the middle ("Who are you?"), given (91% by alpha male) in situations of mild alarm, say, in response to branch-breaking by gorillas not readily visible to other group members or at discovery of a concealed observer.

Infant Calls:

6. Cries. Similar to wails of human infant, sometimes building to shrieks and temper tantrums in highly distressed individuals. Young gorillas seldom cry unless left alone.

7. Chuckles. Rasping expirations emitted during play.

Group-Cohesion Calls:

8. Belch vocalizations. Include a variety of soft-grunting, rumbling, humming, purring, crooning, moaning, even wailing and howling sounds which intergrade in this most complex of gorilla vocalizations. Such calls are voiced most often by stationary gorillas (of all classes) at the end of a long rest on a sunny day or when surrounded by delicious food. Prolonged calls indicate contentment. A group about to resume foraging may croon in chorus. Slightly shortened versions of the belch vocalization serve as a mild disciplinary rebuke to the young.

9. Pig grunts. A series of short, rough, guttural sounds much like the grunts of feeding pigs, expressive of mild aggression and warning. This call is heard most often when gorillas dispute right-of-way or priority of access to food. Although adults of both sexes may *pig-grunt*, the call is heard particularly from dominant males as an assertion of authority.

Other Calls:

Hoot bark. Alerting call expressing mild alarm; group moves away.

Hiccup bark. Similar but less alarm, more curiosity.

Growl. Mild aggression in stationary group.

Pant series. Mild threat within group.

Whine. Given by infants and also by adult males when in danger of abandonment or injury.

Copulatory panting. A series of distinct, fairly low-pitched but loud o-o-o-o sounds produced almost continuously by males during intensive copulation. (Other calls associated with copulation are described under Sexual Behaviour).

The relative frequency with which the above calls are heard in groups habituated to human observers is approximately (1) *belch*, (2) *chuckles*, (3) *pig grunt*, (4) *hoot bark* or *hiccup bark*, (5) *hoot series*, (6) *whine and cries*, and (7) *question barks*. The other calls are relatively seldom heard (frequency of 1% or less). In unhabituated groups *wraaghs*, *hoot barks*, and *hoot series* are voiced with greatest frequency.

Non-vocal Sounds:

Chest-beating, branch-breaking, striking ground, running.

These actions are often combined in the spectacular displays given by silverbacks at the end of a hoot series. The intensity and completeness of the displays depend on circumstances, usually becoming more emphatic as the distance between rival males decreases. The typical complete sequence is as follows:

- (a) hoot series, at the climax of which the gorilla
- (b) rises to stand bipedally,
- (c) grabs a handful of vegetation as it stands and throws it into the air,
- (d) slaps its chest rapidly with alternate blows of its open, slightly cupped hands (fig. 29.2),
- (e) kicks one leg in the air while chest-beating,
- (f) runs sideways for a meter or so immediately after (sometimes during) the climax,
- (g) slaps the undergrowth and tears off branches with his hands during or immediately after the run, and
- (h) thumps the ground forcefully with the palm of the hand.

The full display may continue for as long as ½ a minute, although the actions following hooting occur as one continuous, violent motion finished in 5 seconds or less. Sometimes a silverback interrupts a hoot series by plucking a leaf or herb and placing it between its lips, holding it there until or even while *chest-beating*.

Chest-beating is practiced by all gorillas, beginning as infants, and can be performed in any position, including one-handed while hanging from a tree. But the hollow-sounding "*pok-pok-pok*" is only produced by adult males, whose large air sacs (sometimes apparent as swellings on either side of the throat) amplify *chest-beating* and hooting.

Visual Communication

Strutting walk A very rigid walk, the body held stiff and erect with the arms bent outward at the elbow giving them a curious bowed appearance that emphasizes the power of the long-haired forearms (fig. 29.3). The coat bristles, making the

performer look even larger, and it moves with short, abrupt steps, presenting its side to the receiver, with head turned away except for brief glances (but the performer watches out of the corner of an eye). A dominance display, it must be visible to be effective and gorillas usually perform it in a clearing or while standing on a log. This display is most impressive when performed by rival silverbacks at close quarters, but it is also practiced by infant gorillas, and the form remains the same regardless: it is performed silently without obvious excitement and rarely for more than 15 seconds at a time.

Facial Expressions. As the first man to befriend wild gorillas, reputedly the most fearsome of all beasts, Schaller was understandably alert for signs that would reveal their state of mind. He found their eyes, lips, and mouth to be the most reliable indicators of their emotions, and that he could often predict their response by the eyes alone. The gaze of a relaxed gorilla is bland and the animal surveys its surroundings without obvious attention. The following is a brief catalogue of facial expressions, using the same terms that describe equivalent chimpanzee expressions (see family introduction).

Expressions of Aggression:

Staring ("annoyance face"). Eyes fixed and hard, brows drawn down in a scowl, head often tipped slightly downward, lips pursed and slightly parted.

Tense-mouth face (anger). Staring with mouth half to entirely open depending on intensity of the emotion, the gums and teeth displayed, with the lips curled back. Alternate opening and closing of the mouth is always accompanied by screams and roars. This is the threat display, often combined with a mock charge, reserved for predators, which makes even seasoned observers who know that a gorilla always (?) stops short (provided the observer doesn't run away or counterattack) – bowels turn to water.

Expressions of Fear/Alarm:

Uneasiness. Lips pulled inward with the mouth tightly compressed, eyes shifty (the animal refrains from looking directly at the observer), head often slightly tipped up. Schaller compares this expression (given in response to observers, not to other gorillas) to biting the lower lip in humans.

Pout face (light distress). Lips pursed but compressed or only slightly parted, and brows raised. The animal appears depressed and may whine. Seen, for example, in an infant whose mother walks off without waiting for it, or in captive infants deprived of something they want.

Open-mouth grimace. Not easily distinguished from open-mouth threat (tense-mouth face), especially since emotions of fear and anger are usually combined, but the mouth appears to be held open wider and longer, the corners drawn further back. The head is often tilted slightly back, the brows are raised, and the eyes dart nervously back and forth.

Playful Expressions:

Play face. Open mouth, smiling but without showing the teeth and gums, eyes relaxed.

Olfactory and Tactile Communication

Arousal or "fear" smell

The armpit apocrine-gland odor emitted by aroused silverbacks presumably conveys information about their emotional state (see under Social Organization). As a harem master would hardly "admit" fear to a rival male, it seems more likely that the smell simply signals a state of excitement and alarm, and/or aggressive threat.

Olfactory signals appear otherwise rather unimportant in gorilla communication, except perhaps for odors associated with oestrous (more under Sexual Behaviour).

Social grooming

Described under Social Organization. Comparatively rare among unrelated females and in general less important in gorillas than in female-bonded primates.

As revealed by the distress of orphaned infants when separated from their surrogate mother, nearly continual contact with the mother during infancy is as normal in gorillas as in other apes.

REPRODUCTION

Like other apes, gorillas reproduce slowly. The interval between births averages just over 4 years - unless an infant dies, in which case the mother becomes sexually receptive within a month or less and has been known to have another baby within 9 - 10 months. In a 40 - 50 year life span a female may leave 2 - 6 living progeny. The mortality rate of 35 recorded births in the Parc de Volcans was 46%. Females start cycling at 7 (6 years, 5 months - 8 years, 7 months) and may bear young as early as 8.75 years (12 years at latest), whereas males remain sterile until they become silverbacks at 11 - 13 years of age. Yet a male with a harem of 3 - 4 females has over twice the reproductive potential: 10 - 20 progeny in a 50 - 60 year life span. One silverback, still potent at an estimated 55 - 60 years, had 19 known offspring.

SEXUAL BEHAVIOUR

Of 580 copulations between mature gorillas which were logged during 8000 observation hours in the Parc de Volcans, nearly all were solicited by the female and were performed by the dominant male. The female's behaviour is often "outlandishly coquettish" and that of the male "pretentiously blasé" (Fossey 1982). After making a hesitant approach that can take as long as 15 minutes, the estrous female stands facing him with body turned slightly sideways as if waiting for the male to respond.

If he signals readiness to mount by opening or raising his arms to clasp her, she abruptly turns and backs into the normal dorso-ventral copulation position (fig. 29.4). If he fails to respond, she retreats while looking back at him with a "come hither expression". Adults were never seen to sniff or touch each other's genitals; immature gorillas, however, sniffed an estrous female's rump fairly often.

During copulation, the male either sits upright or leans forward bipedally while holding the female around the waist. The female either squats, hands on the ground or holding the male's hands with one or both of hers, or leans forward on her elbows with rump elevated. Figure 29.4 illustrates the concentrated looks characteristic of copulating gorillas, the male with pursed, the female with compressed lips.

After an interval of $\frac{1}{2}$ to $\frac{3}{4}$ minute of adjusting movements or a motionless pause, thrusting begins and continues for about $\frac{1}{2}$ a minute. The female may also perform deep, slow thrusts, whereas the male thrusts more rapidly, more often, and in longer bouts. Both sexes vocalize, the female more often and for longer (average duration 20 seconds) than the male. She gives rapid, pulsating whimpers, while the male usually makes long grumbling noises lasting 5 - 20 seconds, or pants (see *copulatory panting* under Vocal Communication). Fossey (1982) speaks of soft, plaintive hoots. Vocalizing increases and builds in intensity to longer, howl-like noises which cease abruptly when the mount is broken, usually by the female, which is also the first to move away after separating (89% of 514 copulations). Mounts typically last 1 - 2 minutes but range from 15 seconds to nearly 20 minutes. Both intromission and ejaculation are seldom observed, although ejaculate was sometimes seen on one or both partners following prolonged copulation.

Mating frequency during the 1 - 2 day oestrous of mature females varies from 0.16 to 1.39 copulations per hour, the median for 8 females being 0.3. On 7 occasions, silverbacks were seen copulating with 2 females on the same day (total of 30 copulations). In one instance a male copulated 4 times with each female in 6 hours.

The presence of an estrous female is stimulating to other group members, especially young males, which may mount and attempt copulation with other immature, usually female individuals, but almost never try to mount oestrous females. The dominant male tolerates sexual activity involving preadolescent females and may or may not interfere when subordinate males copulate with adolescent females, which have small sexual swellings, are sexually receptive for 3 - 5 days at a time during irregular cycles (25 - 40 days, average 26 days), but

remain infertile. Females also mount each other and young animals; females in late pregnancy have been seen to mount dominant and subdominant males. Non-pregnant females may respond to mounting by vocalizing and thrusting, especially when mounted by a dominant female.

The characteristic cries of copulating gorillas attract the attention of other gorillas, including other silverbacks, which are most likely to turn up in the vicinity of groups containing estrous females (see under Social Organization). It is under these conditions that most fights and transfers occur.

The presence of lurking rivals makes silverbacks unusually irascible and vigilant, to the point where sometimes a male will move his group under cover of darkness.

PARENT/OFFSPRING BEHAVIOUR

Born after an 8 ½ month gestation period, usually at night, gorillas weigh only about 2 kilos and are quite helpless, yet able to cling to the mother's front with hands and (less securely) short legs and stumpy toes. Though seldom out of arm's reach for the first 6 months, gorillas develop about twice as rapidly as humans. A female captured by poachers at 2 weeks started to crawl, play, grin, bounce up and down, and give chuckling cries at around 8 weeks. At 3 months she began to explore and to manipulate objects rather than simply put them into her mouth, and a month later began making short excursions away from her foster parents. By then she could walk. This is the period when infants normally begin riding their mothers' backs, and by 6 - 7 months they can climb by themselves.

Babies spend increasing amounts of time playing and socializing as they develop. Whether they engage more in solitary or social play depends on the presence of other youngsters. Other group members, including siblings and especially the resident silverback, behave protectively and indulgently toward infants. An orphaned juvenile slept in the same nest with its father. Juvenile females are allowed to groom and carry infants. Older infants and juveniles spend as much time near their father as their mother, after if not before being displaced by the birth of another baby. Weaning usually takes place between the middle and end of the second year.

ANTIPREDATOR BEHAVIOUR

Gorillas subjected to hunting are mortally afraid of man, fleeing for miles after an encounter, the trampled vegetation of their flight path splattered with liquid dung (a sign of extreme fear). Yet the gorilla's defense is based on offense: the charge of the silverback male combined with deafening screams and roars. People with the nerve to hold their ground discovered that it was a bluff: the charge always stopped short-though sometimes only within the last meter. But gorillas have been known to follow through and injure or kill people who ran away. When his

group is attacked, by man, leopard, or another gorilla, the dominant male protects them even at the cost of his own life. Females are equally courageous in defense of their young. Consequently the capture of baby gorillas usually involves the killing of the silverback and the mother, and often other group members as well.

The most dangerous time to approach even habituated groups is during interactions involving silverback males from different units.

SOURCES

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