

1 • Zebras

I stopped to examine these zebras with my pocket telescope: they were the most beautifully marked animals I had ever seen: their clean sleek limbs glittered in the sun, and the brightness and regularity of their striped coat, presented a picture of extraordinary beauty . . .

William John Burchell¹

Plains zebras, mountain zebras, and quaggas were important members of the southern African biota: they interacted with other grazing animals and, together with them, were prey for predators. Collectively, these animals influenced the nature of several biomes.

Zebras and quaggas were well known to indigenous people: they provided them with necessities, such as hides and meat, and featured in their art and stories. Indigenous people distinguished between quaggas and mountain zebras. To the |Xam, the first known inhabitants of the Karoo, they were “||ǃkhwī” and “||kabba,” respectively.² People who spoke the Xhosa language seem to have differentiated between them by their calls: they called quaggas with their barking neigh “iqwarha,” and knew Cape mountain zebras as “idawuwa.”³ The other indigenous people of the region, the Khoekhoe, named both mountain zebras and quaggas “quacha” (sometimes rendered as “qua-cha” or “quakka”).⁴ “Iqwarha” and “quacha” – like the Dutch and English names of “kwagga” and “quagga” – are onomatopoeic, suggesting the animal’s barking cry of “kwa-haa, kwa-haa,” which was often repeated in rapid succession.

After the European colonists introduced horses, which in Xhosa were “ihashe,” to the region, the Xhosa incorporated a reference to the equine family into their name for the barking zebras: “iqwarhashe.”⁵ By differentiating local animals and connecting them to a global family, those names – iqwarha and iqwarhashe – represent the project of taxonomy well, but writ small. Globally, there were several horse-like animals, some striped, some not, and clear names are necessary to catalog the set.

Equines

Carl Linnaeus (1707–1778) developed the modern system of classification that uses a hierarchy of categories to construct closer and more distant affinities. Species are grouped most closely within a genus; the binomial name of genus and species provides a signifier that is unique to the organism. Because many reports of animals came to Linnaeus from all over the world, he had a bigger challenge than Xhosa speakers did with their handful of local species. Linnaeus had to sort out several types of horse-like creatures. Recognizing the similarity between horses, zebras, and asses (wild donkeys), he placed them in the same genus, which he called *Equus*, using the Latin name for horse. Collectively, these animals are referred to as equines. The genus *Equus* is grouped with extinct equids into the family Equidae.⁶

The ancestors of the Equidae can be traced back over 50 million years to animals less than twenty inches (508 mm) tall and with three toes on their hind feet and four toes on their fore feet. The earliest equids browsed on various plants but, with the creation of vast grasslands, their descendants evolved into larger grass-eating animals. The fossil record shows that there were many such species, most of which are now extinct. Equines, animals clearly belonging to the *Equus* lineage, were present in North America about 4 million years ago and their descendants living there died out about 10,000 years ago. Beginning about 3 million years ago, equines spread into South America and, via the land bridge of Beringia, into Eurasia and Africa where their descendants became horses, asses, and zebras.⁷

Equines use their incisors to crop vegetation and their premolars and molars to grind it; their digestive systems enable them to live by eating large amounts of food having a low nutrient content. Their eyes on the sides of their heads afford vision over a wide arc to detect predators, and their senses of hearing and smell provide additional warning of dangers.⁸ Speed to avoid predators comes from highly specialized legs whose digits are reduced to just the middle toe of each foot, which is thickened and greatly elongated; their long legs end in hard, impact-absorbing hooves.⁹ Zebras can run at speeds up to 55 kilometers per hour (34 miles per hour) and horses are even faster.¹⁰ As well as providing speed, strong legs can deliver a powerful kick to a predator or competitor.

DNA evidence reveals the evolutionary history of horses, asses, and zebras. The sequence of four nucleotides, chemical groups that are linked end-to-end to form DNA molecules present in nuclei and mitochondria,

provides key information. Collectively, the DNA of an organism is called its genome and its study is termed genomics. The technique of DNA sequencing enables scientists to compare the order of nucleotides between the genomes of different organisms: an identical or similar sequence of nucleotides argues that two organisms are closely related, or even belong to the same species. Scientists study genomes from both extant (present-day) equines and from preserved material including ancient horse bones preserved in permafrost for over 500,000 years and quagga hides and bones.¹¹ Genomes evolve over time and so the degree of difference between nucleotide sequences of species can help determine the time when they diverged from a common ancestor.

The genus *Equus* diverged into evolutionary lineages leading to asses, zebras, and horses (Figure 1.1). One horse, *Equus ferus caballus*, was

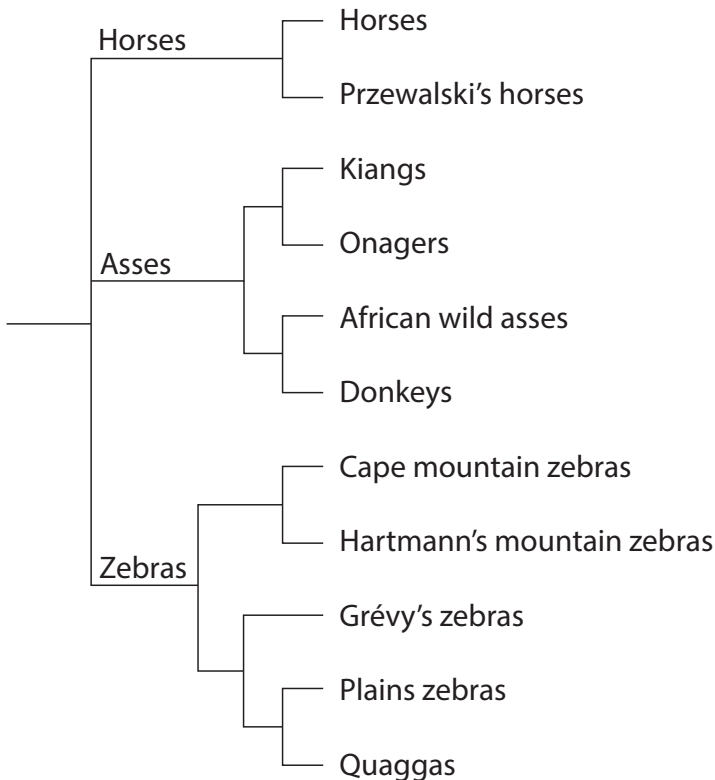


Figure 1.1. Evolutionary relationships between equines showing the divergence of lines leading to horses, asses, and zebras. This figure by the author was prepared by Camille Tulloss¹²

domesticated about 5,000–6,000 years ago and another, Przewalski's horse, *Equus ferus przewalskii*, remains wild and endangered. Asses exist in Asia as *Equus kiang* (kiangs) and *Equus hemionus* (Asian wild asses or onagers) and in Africa as wild asses (*Equus africanus*) whose domestication gave rise to donkeys (*Equus africanus asinus*).

Hippotigris¹³

Linnaeus took the common name *zebra* – derived from a Portuguese word meaning “wild ass” – and used it as the species name for the striped equine that lived in mountainous areas of southern Africa, *Equus zebra*. Boddaert and Gmelin distinguished this species from the partially striped equine of the plains, which they named *Equus quagga* – basing the name on the animal's barking call.¹⁴

Hippotigris, the name Romans gave to zebras, is used to denote a subgenus of *Equus* containing the three zebra species.¹⁵ It is thought that the ancestors of zebras diverged from the ancestors of asses approximately 1.7 to 2.0 million years ago and that the common ancestor of all Hippotigris species separated between 1.28 to 1.59 million years ago into the evolutionary lines leading to the currently recognized species: mountain zebras (*Equus zebra*), plains zebras, which includes quaggas (*Equus quagga*), and Grévy's zebras (*Equus grévyi*).¹⁶

Zebras occur from Ethiopia to South Africa in a variety of habitats from treeless grassland to savanna to open woodlands. They show a slight sexual dimorphism in body size, with stallions usually being a little longer, taller, and heavier than mares. Stallions have thicker necks and possess canine teeth that are used to bite predators and other stallions when fighting; canine teeth are reduced or absent in mares.

Zebras have a black dorsal stripe running from the mane to the tail and a black ventral stripe. Grévy's zebras and mountain zebras have black and white stripes over most of their bodies, although they are broader and fewer in the latter (Figure 1.2). Plains zebras have the fewest stripes, and these are variable in distribution and appearance. Striping characteristics are prominent in the criteria used to identify zebra species, and each animal has distinctive striping that enables even humans to recognize individual zebras. Striped, upright manes and a long tail that terminates in a brush of long hairs are other characteristic features.¹⁷

Zebras prefer to eat grass but will also browse some herbaceous plants and even parts of woody plants and geophytes (rhizomes and corms) if food is scarce. Their incisors crop vegetation and their high crowned premolar and molar teeth have hard surfaces to chew tough plant



Figure 1.2. A Hartmann's mountain zebra and a plains zebra at left photographed in Etosha National Park, Namibia. Photograph by Yathin S Krishnappa. Creative Commons Attribution-Share Alike 4.0 International license. (A black and white version of this figure will appear in some formats. For the color version, please refer to the plate section.)

material.¹⁸ They benefit from microorganisms living in their hindguts that ferment food and so release nutrients that otherwise would not be available. Zebras can live on vegetation with a low nutrient content, but they need to consume a lot of this food in order to survive and consequently they spend much of their time eating, depending on the quality of their forage.¹⁹ One result is that often they need to graze even during the hottest parts of the day – unlike some grazing animals that can seek shade at this time.²⁰ Zebras usually drink water each day and will often walk long distances to reach it. When surface water is not available, they can dig holes to obtain it.

A zebra communicates by making sounds, by body posture, by facial expressions, and by movement of its head, mouth, ears, and tail. Animals often stand close together and groom and sniff each other. Taken together, these signals and interactions can communicate a whole range of messages: greeting, challenging, submission, affection, or readiness to mate. Communication and behavior are important in their social relationships and in surviving predators. Usually gestures of aggression are explicit enough that zebras can avoid fighting, but if not – as, for

example, when a stallion challenges a dominant stallion for possession of his breeding group – animals may bite, rear up, and kick.

Stallions are attracted to mares during estrus and will attempt to mount them. If pregnancy results, a single foal is born after a gestation period of approximately twelve to thirteen months.²¹ Foals have longer, softer, and browner hair than older animals. Befitting an animal born in open country with predators present, a newborn foal, whose legs are almost as long as those of adults, can stand and walk within an hour of birth and can run shortly thereafter. A mare licks and grooms her foal who becomes familiar with the mare's appearance, smell, and vocalizations. During this imprinting period, lasting for several days, a mare will not allow others to approach her foal. A mare will suckle her foal until weaning at between eight and thirteen months of age. Foals supplement milk with grazing when only a few weeks old. A mare may enter estrus within a month of giving birth and so foals may be born annually. Fillies and colts usually leave their mothers when they are one to two years old and become sexually mature by three to five years of age. Colts usually join stallion groups that provide some protection against predators and where the animals have play fights which prepare them for later combat with stallions.

Plains zebras and mountain zebras form breeding groups consisting of a stallion, one or more mares and their foals. Members of a breeding group care for each other, especially by protecting foals when predators are present, and remain together even if the stallion dies or is replaced. Within the breeding group, mutual grooming is an important activity that strengthens social bonds: it occurs between mares and foals, between stallions and mares, and between stallions, but very rarely between mares. After a foal has imprinted on its mare, other members of the breeding group groom the new arrival – establishing a social bond among all. Breeding groups stay together while grazing and walking to find water or vegetation. Often, several breeding groups merge to form a herd (now sometimes called a “zeal” or a “dazzle”). Grévy's zebras do not form breeding groups but have a fission–fusion social organization in which stallions defend their territories but may also at times share these with conspecifics, which may include stallions, mares, and foals; this association provides some protection against lions.²²

Predators of zebras include spotted hyenas (*Crocuta crocuta*), lions (*Panthera leo*), leopards (*Panthera pardus*), cheetahs (*Acinonyx jubatus*), African wild dogs (*Lycaon pictus*), and crocodiles (*Crocodylus niloticus*). Wildebeests (gnus), antelopes, and ostriches that graze with zebras often

provide warning that predators are approaching.²³ When attacked, zebras fight ferociously: the hard, sharp edges of their hooves can deliver powerful blows and their bites are damaging. Although zebras may sleep for up to seven hours a day, they often do so while standing to enable rapid flight and while some sleep one or more members of a herd will remain watchful.²⁴ The social structure of mountain zebras and plains zebras provides some protection against predation: an alarm cry from one will alert others. The animals will form an arc to face a predator that approaches too close, and a stallion will fight it. Members of the breeding group will also gather around a mare with a young foal to protect them.²⁵

Besides predators, smaller organisms also take their toll: worms, flies, ticks, and lice all obtain nourishment from zebras. Particularly problematic are biting flies that annoy, draw blood, and may spread diseases; they are countered by stripes, skin odor, and tail swishing.²⁶ Microorganisms can be debilitating and deadly: bacteria, viruses, and protozoa cause anthrax, African horse sickness, and trypanosomiasis, respectively.²⁷ Yellow-billed oxpeckers (*Buphagus africanus*) and red-billed oxpeckers (*Buphagus erythrorhynchus*) that perch on zebras and eat their ectoparasites are a mixed benefit as they also take blood from sores on the animals.²⁸

Mountain Zebras, *Equus zebra*²⁹

As their vernacular name indicates, these animals live in mountainous areas and at one time must have formed a single population extending in a long swath in the west of southern Africa.³⁰ However, they now exist as two subspecies in geographically isolated populations: Cape mountain zebras (*Equus zebra zebra*) in western South Africa and Hartmann's mountain zebras (*Equus zebra hartmannae*) in Namibia.³¹ Stallions of Hartmann's mountain zebras have an approximate shoulder height of 1,500 mm (59.1 inches) and an average weight of 298 kilograms (657.0 pounds); they are larger and heavier than Cape mountain zebras.³²

Mountain zebras are the only striped equines with a dewlap, loose skin hanging from their throats; they also differ from other zebras in having a "grid-iron" or "fish bone" pattern of stripes on top of their rumps.³³ They are striped all over their bodies, but stripes do not extend to the ventral stripe and so their bellies are white, except for the ventral stripe. In comparison with plains zebras, they have more stripes, and these are narrower, except on the rumps (Figure 1.2). Their ears are larger and rounder than plains zebras, their hooves smaller, and only occasionally do

they make a barking call similar to *kwa-haa*; this sound seems to serve as an alarm call. Their hard hooves are well suited to travel over the rocky ground of mountainous areas but during the rainy season they live on the plains and may even enter desert and coastal areas.³⁴

Births occur throughout the year, with a peak in the late spring and early summer.³⁵ Young foals eat their mother's feces which provides a ready means of acquiring needed gut microorganisms.³⁶ Foals are weaned before they are one year old and leave the breeding group before they are two years old. Fillies may form nonbreeding groups, and colts do likewise, though their groups may be joined by stallions that have failed to secure mares, or that have been ousted from their breeding groups. At maturity, stallions may form a new breeding group with a filly from a nonbreeding group or challenge a stallion for his mares.

Cape mountain zebras are a conservation success story: their numbers had decreased to less than a hundred in the mid-twentieth century, but recent estimates show 1,714 mature individuals distributed on several reserves in South Africa, and the IUCN (The International Union for Conservation of Nature) lists them as being of "Least Concern."³⁷ Hartmann's mountain zebras, with a population estimated to be 33,265 mature individuals, are listed as "Vulnerable" by the IUCN; this designation probably reflects that they are still hunted and that large numbers could be lost if there were a calamitous drought.³⁸

Plains Zebras, *Equus quagga*³⁹

In 1825, the zoologist John Edward Gray (1800–75) named the plains zebra *Asinus burchellii*. He placed this zebra in a different genus, the *Asinus* of wild asses rather than the *Equus* of horses. The species name he took from the explorer and biologist, William John Burchell (1781–1863), who had supplied the British Museum with skins of the animal.⁴⁰ As the genus name *Equus* had precedence, the plains zebra was later given the binomial name *Equus burchellii*. DNA research, however, indicates that quaggas and plains zebras are the same species, with the species name *quagga* having precedence, and so the scientific name for all plains zebras is now *Equus quagga*.⁴¹ The evidence for this conclusion and its implications for rebreeding are important and will be discussed in Chapter 7.

The evolutionary history of plains zebras has produced animals of differing appearance extending over a wide area. About 367,000 years ago, plains zebras possibly living in the Zambezi–Okavango wetland areas (present-day Botswana and Zambia) expanded north to the Equator and

south to the tip of southern Africa.⁴² Over this distance and time, morphological differences developed so that plains zebras vary in size and degree of striping, with both these characteristics forming a cline – a gradient over their range. Generally, the smallest most-striped animals occur in equatorial regions and the larger, least-striped animals are present at the southern end of their range. The smaller size is probably an adaptation to heat as the increased surface-area-to-volume ratio allows better cooling, and the more marked striping protects against biting flies.

Taxonomists had a hard time sorting out plains zebras and many taxa were described. Some plains zebras have distinct black and white stripes, and others have less distinct striping and brown “shadow stripes” within their white stripes. Some animals have stripes over their whole bodies, including their legs, and others have few or no stripes on their legs. Sometimes body stripes extend all the way to the ventral stripe and sometimes they do not and so the belly is white, apart from the ventral stripe (Figure 1.2). In 1936, Angel Cabrera, who had noted variation in coat coloration and striping within a single herd of plains zebras, realized that biologists had named approximately twenty different species and subspecies based on minor variations that occurred between individuals within the same population.⁴³ Reviewing the many descriptions of plains zebras, Cabrera reduced the number of subspecies to four; these did not include quaggas, which he viewed as a different species.⁴⁴

More recently, six subspecies have been recognized: *Equus quagga boehmi* (Boehm’s or Grant’s zebra), *Equus quagga borensis* (Maneless zebra), *Equus quagga burchellii* (Burchell’s subspecies), *Equus quagga chapmani* (Chapman’s zebra), *Equus quagga crawshayi* (Crawshay’s zebra), and *Equus quagga quagga* (quaggas).⁴⁵ Rau, however, questioned whether it is even appropriate to divide up plains zebras into subspecies at all.⁴⁶ This point of view is supported by studies of mitochondrial DNA.⁴⁷ A recent report argues against recognizing subspecies based on morphology and instead identifies ten populations based on their genomics and location.⁴⁸ Two of these populations in South Africa correspond to the subspecies accepted by most taxonomists: quaggas and *Equus quagga burchellii*; the latter is designated as Burchell’s subspecies throughout this book. The name “Burchell’s subspecies” should not be confused with the term “Burchell’s zebra,” which was used to denote all plains zebras when their binomial name was *Equus burchellii*; the name “Burchell’s zebra” is outdated and so appears in this book only when it is part of a quotation.

Sizes of plains zebras are known from measurements taken in the Serengeti (northern Tanzania) and in Kruger National Park (South

Africa).⁴⁹ Adult stallions of *Equus quagga burchellii* in Kruger National Park had a mean body length of 2,800 mm (110.2 inches) measured from the first upper incisor to the end of the fleshy part of the tail, a mean shoulder height of 1,363 mm (53.7 inches) and a mean body mass of 318.5 kilograms (702.2 pounds); values for nonpregnant mares were essentially the same, at a mean length of 2,794 mm (110.0 inches), a mean shoulder height of 1,345 mm (53.0 inches), and a mean body mass of 321.6 kg (709 pounds). Plains zebras in the Serengeti (the subspecies *Equus quagga boehmi*) were considerably smaller: adult stallions had a mean body length of 2,521 mm (99.3 inches), a mean shoulder height of 1,277 mm (50.3 inches) and a mean body mass of 247.8 kilograms (546.3 pounds) and although their mares had a similar mean body length of 2,513 mm (98.9 inches), they had a lesser mean shoulder height of 1,227 mm (48.3 inches) and a lesser mean body mass of 219.1 kg (483.0 pounds).

Some stallions lead a solitary existence, others live together in stallion groups, and those animals that have prevailed over competitors live as part of a breeding group. Mares come into estrus each month and display their readiness to mate, which they may do several times a day.⁵⁰ For plains zebras in South Africa, both mating and foaling usually occur in the rainy season from October to March; pregnancy lasts about twelve months.⁵¹ Mares may enter estrus shortly after foaling and so sometimes foals are born at approximately yearly intervals. A newborn foal weighs on average 33.7 kilograms (74.3 pounds) and has a mean shoulder height of 889 mm (35.0 inches).⁵² A foal can stand and walk within an hour after birth and shortly thereafter it begins to drink its mother's milk.⁵³ At several weeks of age, foals begin grazing but continue to feed from the mother until they are about eleven months old.

Young stallions leave their breeding group between the ages of one and four years to join a stallion group. The members of a stallion group stay together – often within a much larger herd. They interact with each other until they are mature at about four to five years old. At this time, a stallion might successfully challenge an older stallion for his breeding group or abduct a filly. Fillies depart from their breeding group between the ages of 1 and 2.5 years when their estrus attracts suitor stallions; they first give birth at three to four years. If the filly joins a new breeding group, her stallion protects her until she is accepted by the established mares, who are initially hostile to her.

As with other zebras, a plains zebra can communicate by the overall posture of its body, by moving its mouth, ears, and tail, and by

vocalization. Frequent sounds include warning snorts, a blowing sound to show satisfaction, and a kwa-haa barking sound that is often repeated; this cry differs slightly from animal to animal, which suggests that it may help animals recognize each other. Plains zebras also squeal and squeak – both sounds probably indicating that the animal is hurt or afraid.

Plains zebras inhabit a variety of habitats ranging from grassland with few or no trees to open woodlands; they are absent from dense woodlands and deserts. They occur at densities varying from less than one per square kilometer to just over twenty per square kilometer.⁵⁴ Their premolar and molar teeth, adapted to grazing abrasive silica-rich grasses, can chew tough plant material from other sources. In comparison with ruminants such as wildebeests that often graze alongside them, plains zebras are able to live on less nutritious vegetation. Typically, their food has a low nutrient content and so they have to spend much of their time eating.⁵⁵ One study showed that, between sunrise and sunset, lactating females grazed for 63.3 percent of the time, breeding group males for 63.5 percent of the time, and bachelor group males for 46.8 percent of the time.⁵⁶ Although they spend much of their time grazing, sleeping, resting, grooming each other and walking to water, plains zebras also roll in the dust, rub themselves against trees and rocks, and interact with their fellows in play.

Plains zebras frequently graze with ostriches (*Struthio camelus*), wildebeests (*Connochaetes gnou* and *C. taurinus*), and springboks (*Antidorcas marsupialis*). Plains zebras and wildebeests may even eat the same plants – with the wildebeests feeding on the leaves and leaving the more fibrous stems for the zebras.⁵⁷ Collectively, plains zebras, ostriches, springboks, and wildebeests warn each other of the approach of predators by their cries and their evasive movements.

When visiting a water source, plains zebras drink on average 4.7 liters (1.24 gallons).⁵⁸ Although it is often stated that they need to drink water each day, drinking every second – or even third – day has been reported.⁵⁹ Plains zebras usually stay within 12 kilometers (7.5 miles) of a water source and will dig holes to obtain it if supplies are short.⁶⁰ They often spend much time walking to water, with a lactating mare often leading her breeding group in this move.⁶¹ Several breeding groups will travel together as a herd, and larger herds may number several thousand animals. Plains zebras may range over remarkably long distances with migrations of 500 kilometers (over 310 miles) having been reported and with some animals traveling more than 50 kilometers (31 miles) per day.⁶²

Crocodiles kill plains zebras at waterholes, but lions inflict the heaviest toll. Other predators include spotted hyenas, leopards, cheetahs, and African wild dogs. Captain William Cornwallis Harris (1807–1848), a British military engineer who hunted in South Africa, noted the responses of plains zebras to danger:

The senses of sight, hearing, and smell, are extremely delicate. The slightest noise or motion, no less than the appearance of any object that is unfamiliar, at once rivets their gaze, and causes them to stop and listen with the utmost attention – any taint in the air, equally attracting their olfactory organs. Instinct having taught these beautiful animals that in union consists their strength, they combine in a compact group when menaced by an attack either from man or beast; and if overtaken by the foe, they unite for mutual defence with their heads together in a close circular band, presenting their heels to the enemy, and dealing out kicks in equal force and abundance. Beset on all sides, or partially crippled, they rear on their hinder legs, fly at the adversary with jaws distended, and use both teeth and heels with the greatest freedom.⁶³

Ectoparasites such as flies, ticks, and lice vex plains zebras, obtain nourishment from them, and may also cause diseases. Intestinal worms are a problem, as are diseases such as babesiosis, brucellosis, trypanosomiasis, anthrax, and African horse sickness. In spite of predation and diseases, plains zebras can live up to twenty years in the wild and have lived longer in captivity.

Of the three species, plains zebras are by far the most numerous, hence their alternative name “common zebra.” Nonetheless, their numbers are decreasing: in 2002 there were about 663,212 animals in the wild, but a 2016 estimate put their numbers at 150,000 to 250,000 mature animals.⁶⁴ Causes of this decrease include hunting, habitat loss, and climate change. The IUCN lists them as “Near Threatened,” and their fragmented populations make them vulnerable to loss of genetic diversity. Loss of subspecies in particular locations is problematic, for example, the population of Selous zebras in Mozambique declined from approximately 20,000 to less than one hundred in the late twentieth century.⁶⁵

Grévy’s Zebras, *Equus grévyi*⁶⁶

The third species of *Hippotigris*, Grévy’s zebras, are recognizable by their large, rounded ears and by having many thin black and white stripes that are everywhere present except on the bellies and the upper hind legs near the base of the tail (Figure 1.3). They are the largest species of zebras, with a shoulder height of up to 1,600 mm (63.0 inches) and a body

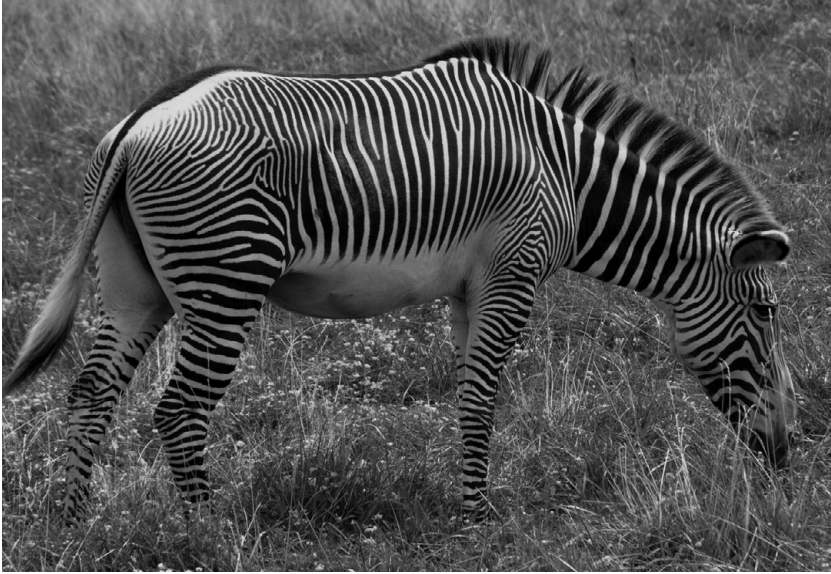


Figure 1.3. Grévy's Zebra. Photograph by T. Bobosh. Creative Commons Attribution-Share Alike 2.0 Generic license. (A black and white version of this figure will appear in some formats. For the color version, please refer to the plate section.)

length of 2,500 to 2,750 mm (98.4 to 108.3 inches); adult stallions range in weight from 352.9 to 430.9 kilograms (771.6 to 992 pounds).⁶⁷

Grévy's zebras had a wide range in Somalia, Ethiopia, and Kenya, but now exist as discontinuous populations in southern Ethiopia and northern Kenya. They live in grassland or shrubland, with grasses as their preferred diet, although they are versatile and will eat other vegetation if grasses are in short supply. They spend much of their time feeding and will range over an extensive area in search of forage and water – which they will dig for in dry riverbeds. As an adaptation to aridity, they can live longer without water than other species of zebras: five days in the case of stallions, but just two days for lactating females. Animals will walk for 10 to 15 km (6 to 9 miles) in search of water and forage and may range over a considerable area.

The social organization of Grévy's zebras differs from the breeding groups of other zebras. Some males live in stallion herds of two to six animals and others are more solitary and set up their territory marked out with urine or dung. However, these animals allow mares and even submissive stallions to enter their territory – although the latter are kept

out if an estrous mare is present. Conflicts between stallions over territory or an estrous mare often involve braying, dominance displays, submissive displays, kicking, and biting. Mares become mature at three to four years and stallions at about six years. As a mare traverses the territory of a stallion in search of water and forage, her urination may attract his attention. If she is in estrus, the stallion's dominance displays and braying may be followed by courtship and copulation, but the pair do not stay together. After a gestation period of approximately 13 months, a single foal is born, usually during the rainy season.

A mare lives with her foal or most recent two foals, and several mares with their foals may group together to form a small herd. The mother suckles, caresses, and protects the foal which she weans by about one year, but which may stay with her until about two years old. After colts leave their mothers, they live in stallion groups or lead a solitary existence. Fillies join other fillies and later will have foals. The fission–fusion social structure of Grévy's zebras differs from the breeding groups of mountain zebras and plains zebras.

The numbers of Grévy's zebras have declined sharply from approximately 15,600 forty years ago to about 2,700 in 2016, and the IUCN lists their status as “Endangered.”⁶⁸ Threats to their survival include predators, diseases, subsistence hunting, and lack of water and grazing which are exacerbated by climate change and competition with the domestic animals of pastoralists. The challenges of conservation are compounded when Grévy's zebras are the preferential prey of lions, which must also be conserved.⁶⁹ An additional problem is that Grévy's zebras can hybridize with plains zebras whose range overlaps with theirs.⁷⁰ The production of fertile hybrid offspring threatens the integrity of their gene pool, which is also at risk from inbreeding because of their low numbers in fragmented populations. Once hunted, Grévy's zebras are now legally protected and, since 2007, the Grevy's Zebra Trust has worked hard and imaginatively for their conservation.⁷¹

Sorting Out Zebras in Southern African History

The diversity of South Africa is evident in its people, its landscapes, and its biota. This richness extended to zebras, whose likenesses were captured by artists, beginning with Bushmen and whose descriptions occur in historic documents. |Xam had different words for mountain zebras and quaggas but Burchell recorded that Khoekhoe used the same word for both species.⁷² References to quaggas or kwaggas might indicate

Equus quagga quagga or one of the other subspecies of *Equus quagga*, or even *Equus zebra*.⁷³ Most people do not ponder the finer points of animal taxonomy: distinguishing between zebras based on their degree of striping or on the presence or absence of a dewlap could hardly have seemed important to those eighteenth- or nineteenth-century observers who lumped together all zebras as quaggas or kwaggas.⁷⁴ Fortunately, some historic accounts refer to mountain zebras as “bergkwagga” and use the name “bontkwagga” or “bonte quagga” (from “bonte” or “bonti,” meaning pied or striped) to distinguish striped plains zebras from the less-striped quaggas.⁷⁵

Traveling from Cape Town to the interior, nineteenth-century explorers, hunters, and naturalists saw mountain zebras, quaggas, and Burchell’s subspecies.⁷⁶ Their all-too-brief accounts provide us with some details of these animals, but much is lacking. Some gaps have been filled by archeologists, whose analysis of bones excavated in caves have provided details of the past lives of zebras. Most remarkably, molecular biologists can unravel their history using the DNA from living cells or ensconced in the hides and bones of their dead. As a result, our understanding of these animals is more substantial than it was just a few years ago. Applied appropriately, this knowledge may aid in the conservation of those zebras that remain.