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Why Serengeti?

A WORLD HERITAGE

In 1972, the United Nations Conference on the Human Environment, in Stockholm, developed the Convention Concerning the Protection of the World Cultural and Natural Heritage.[1] Later in 1972, former US Secretary of the Interior Stewart Udall, a passionate advocate for the environment, who also served as US representative to the Stockholm conference, visited Serengeti. I met him there, took him around the park, and discussed the future. He recounted the events in Stockholm earlier that year: a debate had developed over how to choose World Heritage sites. As a first attempt, delegates were asked to retire for the evening and draw up a list of their top 10 preferred sites around the world. Next day all the lists were collated, and the one with most votes, the top of the list, was the Serengeti ecosystem. It was voted the most important natural area in the world.

Serengeti is outstanding for its biodiversity, its great migrations, and its iconic megafauna of large mammals. It is one of the last remaining relatively intact examples in the modern world of the last Ice Age, or Pleistocene. Why is Serengeti so different from any other place? Why is it regarded as the most important natural ecosystem in the world? All heritage sites are unique in their own ways, so why does this one stand out? We know from paleontology that the main aspects of Serengeti have been around for a long time, some four million years at least.[2] There must be a set of conditions and processes that create special features of

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Serengeti and that result in its persistence over long periods. Over the past 50 years or so, a group of scientists has worked to elucidate these processes, which are governed by what we have termed *principles*. What makes Serengeti both outstanding and spectacular? What are the environmental features that allow a migration of so many animals? What determines the sizes of animal populations and the diversity of species that live there? Indeed, why does it have so many species? These are some of the questions we will consider here as we explore the biology of Serengeti. Using these principles, we can understand the problems facing Serengeti today, and what might happen to it in the future. These principles will also allow us to understand how problems in other areas of the world have developed and, finally, how we can repair them.

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The Serengeti is defined by the area across which the wildebeest migrate. Serengeti is now a household name, the epitome of a wildlife spectacle in Pleistocene surroundings. Surprisingly, it has only recently come to be known thus. It was the lions that first attracted attention, in the 1920s—lions to be hunted by foreigners—and the wildebeest migration was completely unknown. The Serengeti plains were the place to go for the grandest black-maned lions in the world, and there were lots of them to shoot. It was not until the Germans Bernhard Grzimek and his son, Michael, flew their plane over the Serengeti in the late 1950s to document the great migration in their film (and book of the same name) *Serengeti Shall Not Die* that the world first became aware of the phenomenon.[3] The Serengeti is significant because it supports one of the last remaining migrations of large mammals in a relatively unchanged state from the time of the hunter-gatherers, long before the agricultural development that gradually emerged in the 1600s from the Congo, far outside Serengeti, and before the impacts of the modern economic world were felt. It is also a place of singular beauty and remarkable biodiversity: it supports more large mammal species than any other place in the world, and almost as many bird species as the whole of Europe. Despite its relatively undisturbed state, the ecology of the

Serengeti has changed over the past century, and these changes highlight its fragility and sensitivity to climate and human impacts.

Serengeti is a place where biologists can observe nature more easily than most. Its combination of open plains and savanna allows access to most of the area. The large animals are readily observable. One can describe their ecology and behavior using only binoculars. Their populations can be counted accurately. Because of the many decades biologists have been studying the Serengeti, we now understand the causes underlying the huge changes that occurred in the ecosystem both in the distant past and during the past century. By now nearly everyone knows that human impacts on nature are becoming ever more severe, and Serengeti has become a case study documenting these impacts. Long-term studies have shown how political, economic, and social events have driven the ecological changes.[4] Serengeti has become a vital source of information for science on how ecosystems work and how they respond to pressures.

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My involvement in Serengeti began on July 1, 1965, driving south from Nairobi through the Maasai Mara Park to Banagi, the research headquarters of a small band of biologists in the center of Serengeti National Park. My job was to record the bird migrations from Asia, as an assistant to Professor A. J. Cain of Oxford University. He had projects elsewhere in Africa and left me to it for three months. I was given a small roundhouse to live in. My first morning, at dawn, I accompanied the park warden's driver while he read all the rain gauges scattered around the park, a job that was done at the end of each month. It was the first of three days of rain-gauge reading, and in that time we covered the whole of Serengeti, some 20,000 square kilometers.

At the end of those three days, I had seen the Serengeti as few nonnatives had ever done. In the past I had seen something of East Africa, having been raised there, and had visited various game parks. But nothing had prepared me for this experience of wildlife in vast numbers, the extraordinary migrations, the sheer diversity of animals and vegetation,

and the spectacular landscapes. There had to be a reason why Serengeti was such an outstanding place, and I decided to find out, to discover the conditions, the processes and underlying principles that made Serengeti the way it is. But this system, though unique, shares many features with other ecosystems in the world, making it a model for understanding ecological processes.

The principles are useful not just to explain how Serengeti itself works, in its unusual, even aberrant form. In understanding this ecosystem, we can begin to make sense of all other systems by recognizing how they differ from Serengeti; they are the other side of the coin. This book recounts the history of how these principles were discovered.

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Perhaps the best way to begin is with a brief description of the Serengeti ecosystem. Its special geographic features determine its physical environment, climate, water relations, and habitats. Together, these create the conditions that make possible the great migration of wildebeest and other species.

The Serengeti-Mara ecosystem is an area of approximately 25,000 square kilometers on the border of Tanzania and Kenya in East Africa, and its extent is defined by the movements of the migratory wildebeest. This includes many political administrations. The main ones in Tanzania are the Serengeti National Park (SNP) itself, and the Ngorongoro Conservation Area (NCA), which lies east of the park and includes half of the Serengeti plains. North of the NCA is the district of Loliondo. The Maasai Mara Reserve is the main Kenyan administration. This area holds the vital dry-season grazing and water supplies for the migration. South and west of SNP are small game reserves, such as Maswa, Grumeti, and Ikorongo (figure 1.1).

Most of the ecosystem consists of a flat or rolling landscape highly dissected by small seasonal streams that flow into a few major rivers. It is part of the high plateau of interior East Africa. This gentle aspect slopes from the edge of the Gregory Rift in the east down to Lake Victoria in the west, so that all the rivers (except the Olduvai, on the plains)
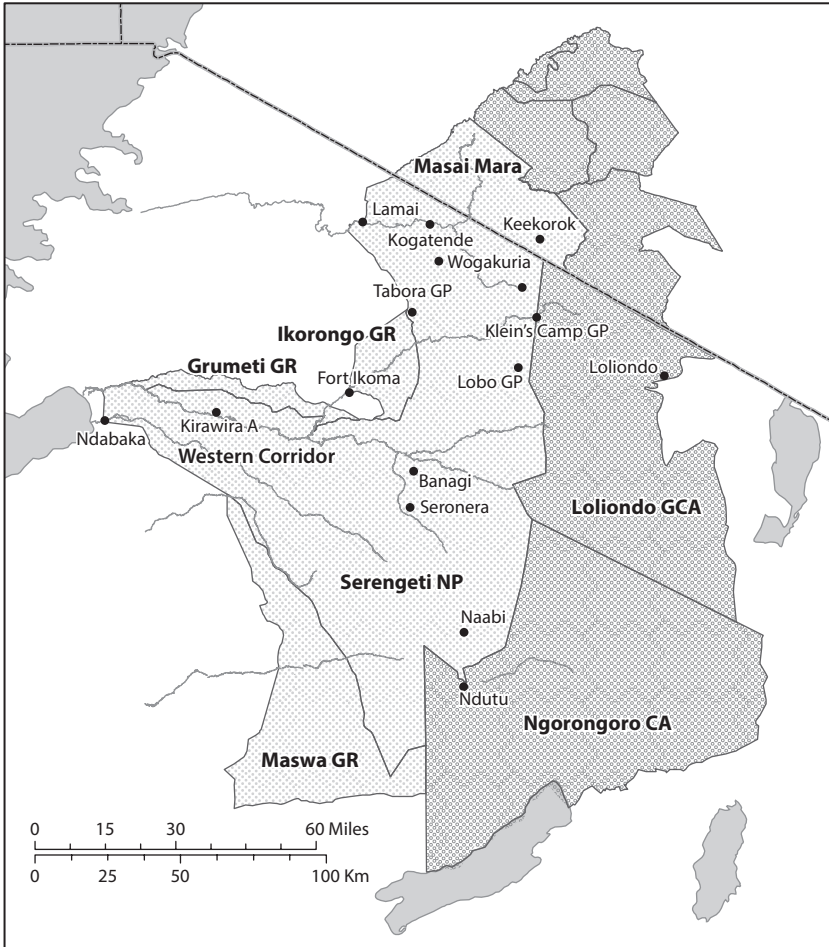
FIGURE 1.1. The main administrative areas and place names in the Serengeti Ecosystem. NP = National Park, GR = Game Reserve, CA = Conservation Area, GCA = Game Controlled Area, GP = Guard Post.

flow west. The highest part of the plains is at an altitude of 1,800 meters, while Speke Gulf in the west is at 1,200 meters.

There are three major rivers, the most important being the Mara, which originates in the montane forests of the Mau Highlands of Kenya. It has until recently flowed year round (see chapter 12), providing the main water supply for the great herds of migrating animals in the dry

season. It flows through the Mara Reserve of Kenya and northern Serengeti, and eventually flows west through the huge Musiara swamp into Lake Victoria at Musoma. The two other rivers are the Grumeti, which originates in the highlands of northeastern Serengeti, and the Mbalageti, which originates on the Serengeti plains. Both are seasonal rivers with only pools remaining in the dry season. Two more rivers originate in southern Serengeti, the Simiyu and the Duma, but only their upper reaches lie within the Serengeti before they flow through agricultural land to Speke Gulf. All other rivers dry out except for a few springs that seep from the base of hills.

Steep, rocky hills occur along the eastern boundary of SNP and between the Grumeti and Mbalageti rivers in the west, forming a backbone to the corridor between the rivers. The Nyaraboro Plateau, with a high (300-meter) escarpment, occurs in the southwest. Because of the generally higher elevation in the east, the hills in Loliondo and the northeast of SNP reach 2,000 meters.

The ecosystem is effectively self-contained, enclosed by natural boundaries on all but one side. The eastern boundary is formed by the escarpment of the Gregory Rift and the base of the Crater Highlands. The south is bounded by the edge of the Serengeti plains and in Maswa by the appearance of numerous kopjes (rocky outcrops). In the west, the corridor, which is largely an alluvial plain formed by the rivers, is bounded on both its south and north by higher ground—now agricultural land—and by Speke Gulf. The west side of the northern extension of Serengeti to the Kenya border is an artificial boundary set by agriculture. Within Kenya, the Mara Reserve is bounded by the Isuria escarpment, the Loita plains, and the Loita hills (figure 1.2).

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The Serengeti ecosystem is (very roughly) a square, with the treeless plains covering the bottom right quarter, about 5,000 square kilometers. They were formed by dust deposits from the volcanoes of the Crater Highlands 4 million years ago. To understand how this happened, we have to go back to the Miocene, some 14 million years ago, when eastern
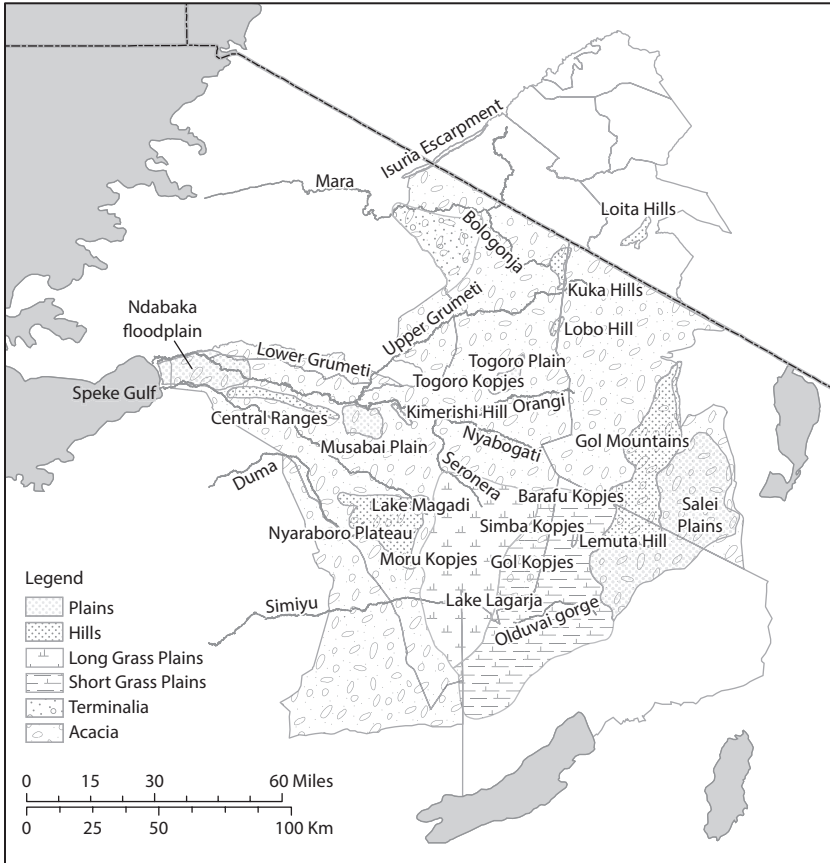
FIGURE 1.2. Topography and habitats of the Serengeti ecosystem.

Africa began to split apart due to plate tectonics—the same process that split Africa from South America starting 100 million years ago. Africa is still breaking apart and in a few million years will be two continents. The split is developing down a rift, the Great Rift Valley, from the Dead Sea in the Near East through Ethiopia to East Africa. In East Africa this rift splits into two arms (figure 1.3). The western arm, called the Albertine Rift, runs along the western borders of Uganda, Tanzania, and Mozambique. Within it lie the deep lakes Albert, Tanganyika, and Malawi. The eastern arm, the Gregory Rift, runs through the middle of Kenya and Tanzania. The edges of each rift are uplifted so that the land between
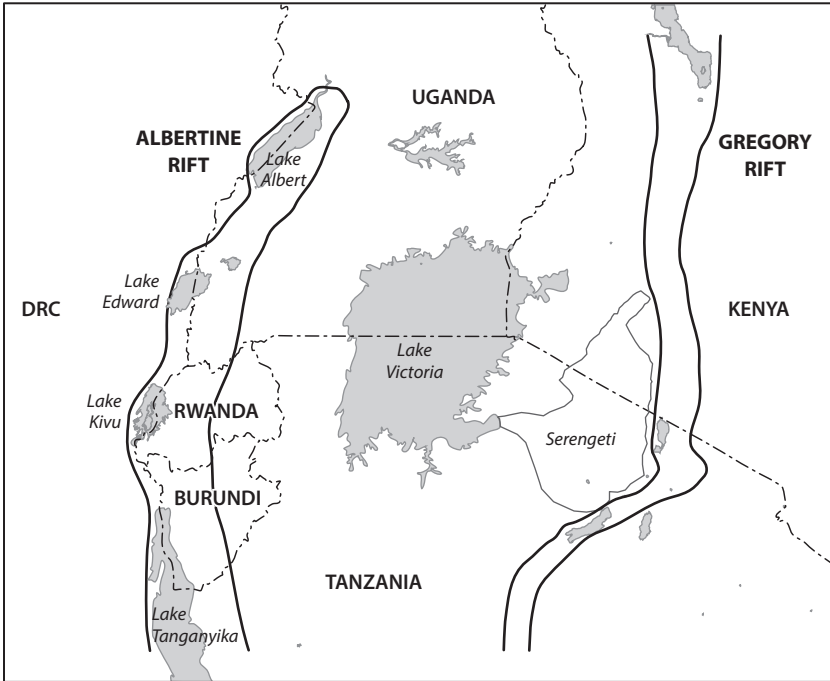
FIGURE 1.3. The rifts and lakes of East Africa.

the two forms a shallow basin. Lake Victoria is impounded in this basin, essentially a vast and shallow puddle only about 65 meters deep at its greatest depth. At 65,000 square kilometers, it is huge, the largest lake in Africa and the third largest in the world after Lake Superior and the Caspian Sea (which is in fact a lake). It is some 200 kilometers across both west and north.

Over time the rifting resulted in volcanoes, and the Crater Highlands of Ngorongoro, made up of several different volcanoes, developed. These were very active four million years ago, during the Pliocene period. Prevailing winds from the Indian Ocean in the east blew the dust westward; it settled out, deeper close to the volcanoes and gradually becoming shallower as it was blown farther west. Eventually this dust hardened into an impenetrable layer of calcium, a hardpan (called calcareous tuff) close to the surface. Tree roots cannot penetrate this, and so cannot take hold, but grasses and herbs, especially creeping ones, can establish themselves.

The volcanic soil was rich in nutrients, especially nitrogen, phosphorous, and calcium, and the creeping plants became highly nutritious. The volcanoes are quiet now, but one, Oldonyo Lengai, is still active, with significant dust fallout in 1966 and 2007. The Ngorongoro Crater itself is a caldera, the sunken base of an old volcano.

Far enough west from the volcanoes, the hardpan becomes sufficiently thin and broken up that trees can get their roots through and establish themselves. This produces something unusual in ecology, a very narrow boundary between trees on one side and no trees on the other. This boundary, only a few meters wide, runs along the northern, southern, and western sides of the plains. Seronera, the park headquarters, lies in the corner of the western and northern boundaries. The geology from the edge of the plains westward and toward the center of the park is largely ancient granite with sediments from hills and rivers.[5]

Climate

There are two special climatic features that determine the Serengeti environment. First, the Crater Highlands in the southeast are sufficiently high (2,400 meters) that they impede the prevailing winds from the Indian Ocean, causing a rain shadow on their western side, where precipitation is scarce. The far-eastern Serengeti plains, therefore, are semi-arid, receiving only 500 millimeters of rain per year. Sand dunes are gradually moving across that region. The second important feature is Lake Victoria, in the west. This lake is so large that it creates its own weather system; rainstorms develop over the lake and affect the west and northwest of the ecosystem, even during the dry season. So there is a wet northwestern region and a dry southeastern region, producing a marked gradient in rainfall. It is this gradient that drives the migration and ultimately determines the working of the entire ecosystem.

Serengeti is a highly seasonal environment, with rainfall being the major influence. Rain is determined by the position of the sun. Serengeti is near the equator, lying just two degrees south. The sun passes over it on its way south in September and on its way north in March. About six weeks after the sun passes, a band of heated air, the Intertropical

Convergence Zone, follows the sun and draws in wet air from the Indian Ocean. As a result, there are two wet seasons, a shorter one in November and December and a longer one from March to June. Both seasons are variable, the shorter one often absent, but sometimes the two merge to form one long wet season—as occurs when there is a strong El Niño event in the Pacific Ocean. There is a long dry season from July to October. July is the driest month, giving way to storms that become more frequent in subsequent months in the northwest of the system. In addition, Lake Victoria contributes rain from storms generated by heating over the lake.

Habitats

We can think of Serengeti as having three major habitats, which, by coincidence, lie along the rainfall gradient (figure 1.2). First, there are the plains in the southeast, which as already mentioned are formed by a calcareous layer under the soil derived from volcanoes long ago. This layer prevents trees from growing, and so the plains are open grassland. However, there is also a gradient of grassland types within the plains. The far-eastern plains are very short grasslands, composed roughly of 40 percent grasses and sedges, 40 percent small flowering herbs, and the rest bare ground. All these plants are heavily grazed, though they grow close to the ground as protection from being eaten. In the middle of the plains, the grasses are longer (30 centimeters), mixed also with flowering shrubs; these are the intermediate plains. To the west and north lie the long-grass plains, where the grasses grow up to a meter. The Salai plains form the northern half of the eastern grasslands in the Loliondo district. They are very dry and contain sand dunes, most of them covered with tussock grass, except for some that are still moving.

The second habitat, the acacia savanna, starts abruptly at the edge of the plains as the effect of the volcanic soil disappears. The majority of the savanna is formed by many species of African acacias, often as single-species stands. Each has its own preferred position along a gradient of drainage. The gently rolling landscape results in well-drained ridgetops with sandy soils. The soil type changes progressively down the slope

FIGURE 1.4. The short-grass plains at Gol Kopjes with wildebeest, May 1971.

until poorly drained and even waterlogged silt soils are found at the bottom, near rivers and drainage lines. The African acacia species lie along this gradient—umbrella trees (*Vachellia [=Acacia] tortilis*) prefer the tops, stink-bark acacia (*V. robusta*) prefers mid-slope, while yellow-fever trees (*V. xanthophloea*) like wet soils near rivers, and gall-acacias (*V. depranolobium, V. seyal*) live in waterlogged, swampy soils. These are just a few of the many tree species that occur here. The grass layer is composed of species similar to those on the long-grass plains, but under trees there are other species together with many flowering herbs. The grass layer in the savanna is much richer in species than on the plains. Along riverbanks and around kopjes are shrubs that form thickets—favorite hiding places for predators (figures 1.4, 1.5, 1.6).

The third major habitat is the broad-leaved woodland of the far north-west, composed mainly of trees of the genera *Terminalia* and *Combretum*. The soils are derived from granite and, though poor in nutrients, support tall grasses (up to 2 meters) and many different species of shrubs.

There are also special habitats. The western end of the corridor was, until a few thousand years ago, under Lake Victoria; it is now a flat

FIGURE 1.5. Savanna with dense stands of stink-bark acacia, facing west to Lobo Kopjes in background, November 2005.

FIGURE 1.6. Broad-leaved *Terminalia* woodland with tall *Hyparrhenia filipendula* grassland in northwest Serengeti, March 2005.

floodplain, the Ndabaka, with alternating clay soils and sandy ridges (old beaches). It floods during the rains. The hills in the center of the park, on the Nyaraboro plateau, and along the eastern boundary are stony or have thin soils. Species of *Combretum* are found on lower slopes, but a mixture of small acacias and shrubs grow higher up. On the higher hills of the northeast, such as Kuka Hill, the elevation results in montane forest, a relic of that on the Crater Highlands and the Loita hills in Kenya. Most of this forest has been destroyed by fire over the past century, and the hills are now covered by grassland, but small patches of forest remain in gullies where fire cannot reach.

The Mara River supports riverine forest, which is an extension of the montane forest downstream from the highlands in Kenya, where the river has its source. This is closed-canopy forest maintained by a high water table from the river. It can be half a kilometer wide but more usually is 50 meters or less in width. There is evidence it was much more extensive in past centuries. The Grumeti and Mbalageti rivers along the western corridor also support forest, but this is forest of a completely different type. It is a subset of the lowland Congo forest and has almost no overlap in tree species with the Mara montane forest.[6] The Serengeti thus supports two major forest types, only 50 kilometers apart.

The rocky outcrops, or kopjes, found in the eastern half of the ecosystem are granite intrusions and are surrounded by a matrix of volcanic rocks. These small islands of rock support dense shrubs and broad-leaved trees such as marula (*Sclerocarya birrea*) and fig trees (*Ficus* species). Vegetation is scarce on the kopjes of the eastern plains but lush on those at Moru, an area of large kopjes at the western edge of the plains in the south of the park. Kopjes are small in area but are an important and special habitat for animals.

The Animals

The most numerous big mammals in the Serengeti are the ungulates. These are large hoofed animals such as antelopes, zebra, buffalo, giraffe, rhinoceros, and hippopotamus. Every year during the great migration about 1.5 million wildebeest, together with 200,000 zebra and half a

million Thomson's gazelle move around the system—over 2 million animals in all (figure 1.7). They all converge on the plains in the wet season because that is where the best food is. The grasses of the plains have the highest protein in the whole of Serengeti, but calcium and phosphorus are also high. The animals move around the plains following the rainstorms and the growth pattern of the grasses.[7] The three migrant grazers, however, stick to their own kind, with only a small overlap in their distributions, each taking advantage of the different heights of grass. As the plains turn green with the first rains, usually around December, the Thomson's gazelle arrive first, feeding on the short new growth. Then, as the grass grows a little taller, say 15 centimeters, the wildebeest arrive and displace the gazelle, which now move farther east to the short-grass plains. Eventually the zebra arrive, and they confine themselves largely to the intermediate grass plains. This sequence of zebra on the western plains, wildebeest in the middle, and gazelle in the east moves farther east in lockstep as the wet season progresses and the plains become wet and waterlogged in April. They all move back west in the reverse order, with zebra going first, when the plains dry out in May or June. However, in January and February there is quite often a dry period (between the two rains), and in that case the whole sequence moves south and southwest into the Maswa Game Reserve, a 2,200-square-kilometer area bordering the Serengeti National Park. The reserve is a vital retreat at this time of year. One other species also migrates. This is the eland, the largest of the antelopes (males can stand 1.6 meters at the shoulder and weigh more than 600 kilograms). Some 15,000 of them move onto the plains in the wet season, feeding on herbs and also grasses when the latter are green (figure 1.7).

June sees the migration moving west and north. It is at this time of year that the herds graze the long grasslands. They move slowly—both because it takes time to graze long grass and because they are wary of predators—and so bunch up and form the dense masses that have become famous from photographs. Wildebeest dictate the movements of the other species. They eat down the grass and provide a food niche of short grass for the gazelle that follow behind.[8] Zebra are often found close to the wildebeest, probably because of safety, but they must stay

FIGURE 1.7. Wildebeest migration, Seronera, June 2004.

in front because they need a greater bulk of food than the wildebeest. A picture of the great herds would show a front fringe of zebra, a mass of wildebeest, and then a dispersed scattering of gazelle behind.

Once the herds reach the woodlands, this pattern breaks up and smaller groups of wildebeest and zebra make their way west and north during July and August. Thomson's gazelle stay behind in the central woodlands, and by the later dry season there is little overlap with the other two species. By the end of the dry season (September, October), the wildebeest are in two major groups, one in the corridor between the Grumeti and Mbalageti, the other in the northwest of Serengeti and in the Mara Reserve of Kenya. Eland move north to the *Terminalia* woodlands, where they feed on the more abundant shrubs.

The beginning of the rains, in November, brings the migrants south and east again toward the edge of the plains. However, the rains usually begin with scattered thunderstorms, which cause the herds to spread over most of the woodlands in search of local patches of green food.
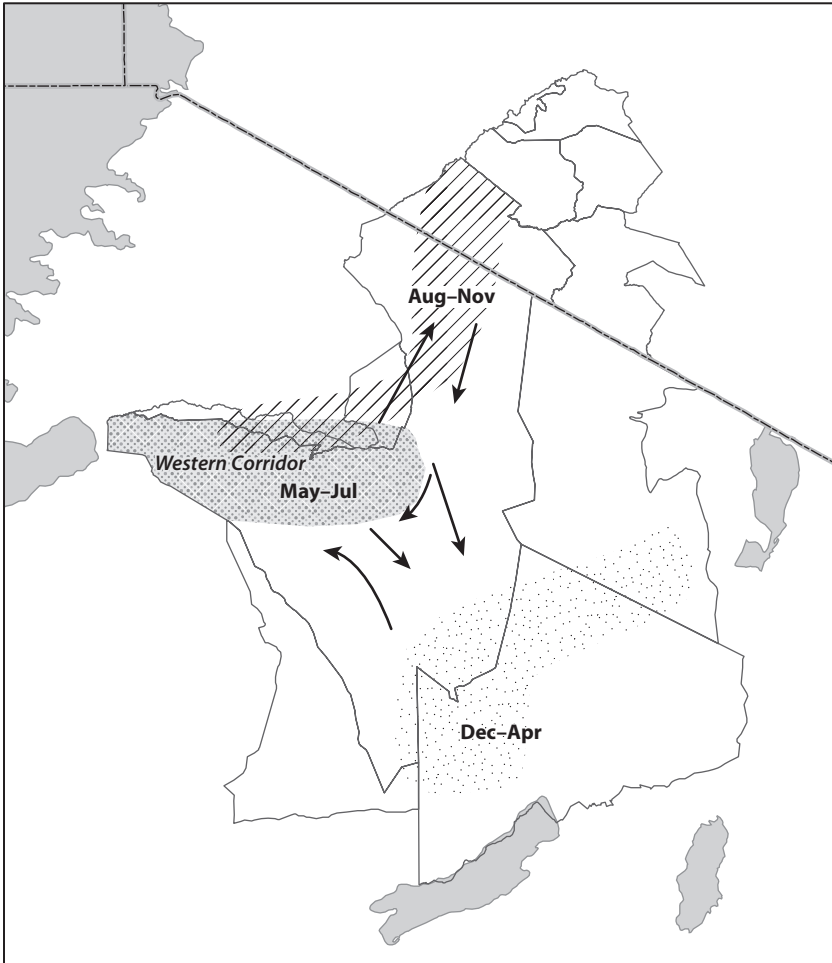
FIGURE 1.8. The seasonal distribution of the migratory wildebeest and zebra. In the wet season (December–April) they are on the plains; in the dry season (August–November) they are in the corridor and north into Kenya.

They are at their most dispersed at this time, only congregating again when the rains become more consistent and the herds can once again move onto the plains (figure 1.8).

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The distinction between those we call *migrants* and those we call *residents* is more of scale than of absolute differences. All species move with

the seasons, but whereas the migrants move hundreds of kilometers, the residents usually move only a few.

The commonest resident antelope is impala, the quintessential animal of Africa. Paradoxically, it is the only one of its kind; it has no close relatives. Impala live in herds of 10 to 200, all females and youngsters, and one male. All other males are forced out to live in large bachelor groups.[9] Impala live wherever there is savanna, feeding on shrubs, herbs, and green grass, never venturing onto the plains.

Topi and kongoni are both close relatives of wildebeest, all being members of the family called Alcelaphinae, and they all eat grass almost exclusively. Both species are sedentary, topi living on wet grasslands in large groups of sometimes several thousand in the western corridor, while kongoni keep to the eastern woodlands and long-grass plains, where conditions are much drier. There are no kongoni in the corridor. Both species overlap in the center and northern woodlands, living together in small groups.

There are several species of antelope that live in more restricted habitats. Water-loving antelope include waterbuck (at 270 kilograms and more, a male waterbuck can be larger than a wildebeest) and the smaller common reedbuck, which is abundant in all tall grassland including the plains but rarely seen except along rivers. The rare mountain reedbuck is found only on the tops of the highest hills. Bush or forest antelope include bushbuck wherever there is thicket along rivers and greater kudu in the kopjes of Maswa. Lesser kudu are found in the montane forests of the Loita hills, which are not part of our system, but it is possible they are in the forests of the Serengeti highlands in Loliondo, yet to be discovered.

On the Salai Plains we find the desert-adapted beisa oryx. These are rare and may now be extinct in our system. Related to these is the roan antelope. They prefer, strangely, the low-nutrient granitic savanna typified by broad-leaved woodland. They were once abundant over the whole of northern Serengeti and Mara, some associated with the central hills such as Banagi, but they have since disappeared. One small group is being nurtured in the Grumeti Reserve and another in the Maswa Reserve. Another species that prefers the broad-leaved woodland is oribi, a small antelope that lives singly or in small groups,[10] mostly in the far northwest. Other small solitary antelopes include grey duiker in

similar broad-leaved habitat, and steinbuck, which prefers dry acacia savanna.

African buffalo were also abundant, reaching 70,000 in the mid-1970s, but after the border closure with Kenya in 1977 rampant poaching reduced their numbers to 20,000 by the 1990s. They have now returned to original densities except in the northwest, where poaching continues.[11] Buffalo live in the savanna in herds of up to 1,500; they feed on long grass and need daily access to water. Giraffe are also ubiquitous in the savanna. Numbers are not well known, although we think there are about 8,000. Megan Strauss considers that they may be declining due to poaching.[12]

Rhino were once common over the entire Serengeti, including Olduvai Gorge. But again, beginning in 1977, the same poaching effectively exterminated the rhino and only a few remain in the south and in northern Serengeti and the Mara Reserve. Careful guarding of these few has kept the population alive since 1990, but they have not increased much.

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Serengeti was first famous for its lions; hunting expeditions of foreigners would camp at the edge of the plains on the Seronera River because there were so many lions in the vicinity. It was the extermination of lions that led to the first small part of Serengeti becoming a protected area in 1930. Only in 1951 was the larger park legally demarcated. The Seronera River is still the best place to observe lions, although they range over the whole ecosystem.[13] Leopards live throughout the savanna and can also be found around the kopjes in the long grassland wherever there is dense vegetation. They are always secretive and difficult to see. Cheetahs are seen most frequently on the plains, but they occur in the savanna as well. There are also several small cats—serval, caracal, wildcat—but they are not often seen.

Hyenas are the most abundant carnivores in the system, some 7,000 of them.[14] They live in groups on the plains and hunt large ungulates together. They follow the migrating herds around the plains and some way into the woodlands, perhaps 50 kilometers. Once the herds get beyond

this, hyenas that live on the plains do not follow. There are hyenas living throughout the savanna, hills, kopjes, and even forest; these are usually solitary and scavenge or feed on small animals. Hyenas that live in packs are also found on the larger grasslands within the savanna, such as those at Musabi, Togoro, the Mara Reserve, and the Loita plains in Kenya.

Several species of the dog family are also found in the Serengeti. The best known are wild dogs, which were once found throughout the savanna and plains. Strangely, European hunters and wardens disliked them and shot as many as they could (as they did hyena)—despite the area's being protected. Then, starting in the late 1960s, wild dog numbers within the ecosystem began a decline, which was linked to the increase in larger predators and the spread of disease from domestic dogs (described in chapters 5 and 12). The decline ended with their disappearance in 1992. A few packs have since been discovered on the far-eastern edge of the ecosystem; they had probably always been there, undiscovered, but may have come in from elsewhere. Some of these animals have since been reintroduced to the western corridor and are thriving. There are four other dog types: the golden wolf (previously known as the golden jackal) is found mainly on the short-grass plains and around Ndutu; the black-backed jackal is common in the savanna; and the side-striped jackal, which is solitary, is seen only occasionally in both long-grass plains and savanna. The bat-eared fox, closely related to dogs, specializes in eating dung beetles—its large ears allow it to hear beetle larvae underground. It lives in holes throughout long-grass plains and the open areas of savanna.

The Serengeti also hosts many species of small carnivores, most of which feed on rodents and insects. These include members of the weasels (family Mustelidae) such as the zorilla and honey badger; six species of mongooses (family Herpestidae); and the civet, common genet, and spotted genet (family Viverridae).

The ground pangolin (order Pholidota) also occurs in low numbers. Being nocturnal, it is hardly ever seen, but since it is one of the rarest (and most threatened) mammals in the world, it is of special interest.

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Recent taxonomy using comparisons of DNA (genomes) has revealed an ancient group of mammals that evolved when Africa was cut off as a great island, some 100 million years ago, at the dawn of the age of mammals. They are called *Afrotheria*, and they include the elephants, hyraxes, aardvark, and elephant shrews: a truly African group.[15]

Bush elephants (those that occur in the Congo forests are now considered a separate species of the smaller forest elephant) occur in savanna and long-grass plains and number about 3,000. They could be considered as migrants. There are two and possibly three populations, a northern group based on the Mara River and its forests in the dry season—including both the Kenya and Serengeti portions—and a southern group based on the Duma and Simiyu rivers and rivers in Maswa. In recent years, a third group has appeared in the western end of the corridor based on the Grumeti and Mbalageti rivers. The northern group moves south about 150 kilometers toward Seronera in the rains. The southern group moves east about 50 kilometers to Moru, and even across the plains to Lake Lagarja when it is wet. The western group appears to remain more sedentary in the corridor.

Hyraxes are rabbit-sized animals that live in kopjes and forest trees. Two species—rock hyrax, which feeds on the ground, and bush hyrax, which feeds in trees—live together in the crevasses of kopjes throughout the savanna and a few kopjes on the edge of the plains where there is enough shrubbery. The third species, the tree hyrax, lives only on the Mara River in the holes of large riverine trees.

Perhaps the most unlikely relative of the elephant is the aardvark. With its strange, tubular teeth, long snout and tongue, and long digging claws, it is supremely adapted to opening up mounds to eat ants and termites. It occurs everywhere there are termite mounds, digging into these from the side to access the nests and using its long tongue to lick up the insects. It is nocturnal, solitary, and rarely seen. But its influence on the ecosystem is large, for many species use the vacant termite holes as their houses.

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Among other animals, biodiversity is very high in some groups. More than 600 species of birds flourish because of the high diversity of habitats, and many are influenced by the wildebeest migration. For tourists, birds are one of the more obvious features of the Serengeti. In contrast, rodents are not obvious, but they are also diverse; some 30 species occur, and many of the small carnivores and birds of prey depend on them.

Insects are not yet well described, but we have found approximately 180 species of butterflies, 100 species of dung beetles, and 70 species of grasshoppers. The insect fauna support the majority of the bird species. In contrast, both the reptile and amphibian fauna are not diverse. There are only a dozen species of lizards, 20 or so of snakes, and 30 of amphibians.

People

Humans have been involved in the Serengeti ecosystem for probably the entire length of human evolution. As described earlier, relatives of modern human beings lived around the lake now called Olbalbal, at the foot of the Crater Highlands, 1 million years ago. In the millennia since, humans likely persisted first as scavengers following the great migrations, and then as hunters. Artifacts found at Olduvai, Lake Lagarja, show they lived and hunted around the lake. A hand axe that could have been 100,000 years old was found on a ridgetop in the *Terminalia* woodlands. Other artifacts eroding from the banks of the Mara River at Kogatende could also be tens or hundreds of thousands of years old. Clearly humans and their earlier relatives have been in the system for a long time. However, we have no knowledge of what impact they may have had in shaping the system; it was simply too long ago. We may surmise that their populations were so low that their predatory impacts on the ungulates would have been quite small.

The most important impact of early humans was the use of fire. There is a scrap of evidence to suggest that fire may have been present 1 million years ago, but this could have occurred through lightning strikes.[16] Nevertheless, humans used fire early on, meaning that the ecosystem has been subjected to burning for hundreds of thousands of years; humans

may be the reason why savanna vegetation has evolved to become fire adapted (see chapter 8). Large savanna trees such as *Acacia* species and broad-leaved *Terminalia* and *Combretum* can withstand burning. Even hot fires that scorch leaves merely result in shedding of dead leaves and regrowth of new ones. Young trees (less than 2 meters tall) within the reach of fires are usually scorched back to ground level. But they do not die; most have large rootstocks containing a substantial food reserve, which the plant uses to sprout again in the next rainy season. Eventually, some of these small trees manage to escape fire and grow into mature trees to maintain the savanna. Some shrubs and bushes, such as *Ormocarpum*, have evolved corky bark that withstands burning. Some plants take refuge within the dense undergrowth of other species. The candelabra euphorbia tree (*Euphorbia ingens*), for example, cannot grow in open grassland because its fleshy, mesophyllic stems are rapidly destroyed by fire. However, it starts life by growing within the lower thicket at the base of the umbrella acacia (*V. tortilis*). The young candelabra grows straight up through the top of the acacia, then branches out to form the characteristic mature tree, while killing the acacia, probably to improve root competition. Other small flowering herbs also take refuge in thickets where fire cannot penetrate. Thus does fire promulgated by humans shape the Serengeti plant community.

Humans, of course, have a pervading and all-encompassing impact on the ecosystem through their influence on global climate change (see chapter 13). These are relatively recent events. In this tropical system just off the equator, climate change manifests more by altering rainfall than temperature. Although increases in temperature have been detected,[17] they are small. Much more important is the prospect of major fluctuations in rainfall. As elsewhere in the world, the highs and lows are becoming more exaggerated, in this case creating longer dry periods and greater floods. The worst drought of the twentieth century occurred in 1993. The greatest floods, exceeding all records, took place in 2019–2020. These events are strongly influenced by what is known as the Indian Ocean Dipole, the heating system in the Indian Ocean that determines the rainfall in Africa and elsewhere. At the same time, the El Niño Southern Oscillation, driven by heating of the western Pacific Ocean

(similar to that of the Indian Ocean), is showing more frequent and more extreme events, which affect nearly all components of the Serengeti ecosystem[18] (see chapter 8). These impacts on the Serengeti cannot be avoided.

In contrast to these long-term natural impacts, the shorter-term impacts of humans during most of the nineteenth and twentieth centuries have been largely confined to small-scale bushmeat hunting,[19] with the exception of the ivory trade (see chapter 4). The considerable historical evidence[20] shows that while hunter-gatherers were present in small numbers over the past 300 years, there was no agricultural settlement in the main part of the Serengeti ecosystem, the savanna, because of the tsetse fly. Agricultural tribes arrived from west of Lake Victoria in the sixteenth century but did not inhabit the eastern shore until the nineteenth century. Even then, they remained far to the west of the present Serengeti ecosystem. Only toward the end of the nineteenth century did agriculture arise in a narrow strip north of the corridor (and hence not in the ecosystem) along the Bunda–Ikoma road, to which it is still limited today. While this strip is suitable for agriculture, the soil and water in the area to the south, inside the Serengeti, will not support crops. Similarly, to the south, the Wasukuma people are limited to higher ground outside the current Serengeti boundaries, just as they were in the nineteenth century. To the northwest, the Wakuria people were limited to areas close to what is now Musoma, and nowhere near Serengeti, moving east only in the 1950s but remaining outside the tsetse belt in Serengeti. To the east, Maasai pastoralists were recent arrivals in the mid-1800s, and used only the far-eastern plains to avoid both the tsetse and the wildebeest. Only later, in the 1930s, did they move west toward Moru in the dry season for temporary grazing but retreated when the wildebeest returned. Overall, modern humans have had little impact on the Serengeti savanna in recent centuries.

Because of these circumstances, the Serengeti ecosystem becomes one of the most suitable areas in the world to act as a baseline for assessing the impact of humans on their own habitats. Agriculture being the single greatest disturbance to ecosystems, there is a concern that it could ultimately destabilize the systems on which humans depend.

Thus, for the benefit of future generations we would be well advised to both detect and monitor these human-induced perturbations. To detect disturbance by humans it is necessary to have a number of areas without that human impact in order to compare them with areas of agricultural development. These are the controls, the baselines that act as reference points. They are in fact the insurance policy for humanity in the future. It is for this purpose that the Serengeti has been studied and described here. We are not suggesting that Serengeti (or indeed any other baseline ecosystem around the world) is or even should be a pristine environment, without humans; probably no such place exists. Serengeti has been influenced by humans since the dawn of humankind. But it is the modern impacts of agriculture, forestry, and urbanization that we want to measure by comparing with areas free of those impacts.

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This is just a rough outline of the immense richness of the Serengeti ecosystem. The variety of species is enormous, encouraged by the diverse habitats and the impact of the great migration itself. This is the Serengeti as it now stands. It has arrived in this form through a long series of changes caused by events over the past 200 years and more. These events were crucial in allowing us to understand how the Serengeti worked. The first of these formative events was the appearance of the viral disease rinderpest. The effects of this disease proved to be fundamental not only for understanding Serengeti, but also for shaping the ecology of the whole of Africa, probably for centuries.

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