CHAPTER 15

Trophic Cascades in African Savanna: Serengeti as a Case Study

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In this chapter, we examine the role of trophic cascades in tropical savannas, with particular attention to the Serengeti ecosystem of East Africa. Africa is perhaps the last place where the Pleistocene megafauna are still largely intact and thus where "natural" interactions can be observed among animals at the top of the trophic web. Serengeti presents an unique case study because of some 50 years of detailed information on current trophic processes supported by extensive knowledge of the region's paleoecology going back 4 million years (Sinclair et al. 2008; Peters et al. 2008). The Serengeti ecosystem also features megaherbivores, in particular elephants (*Loxodonta africana*), that have outgrown their predators and so are unlikely to be predator regulated like the many smaller herbivores in their community (Fritz et al. 2002). Here we consider how these megaherbivores of Africa create or modify trophic cascades while also discussing the contributions of apex predators, birds, migratory herbivores, small ungulates, forests, and grasses to top-down and bottom-up processes in the Serengeti ecosystem.

Because plants form the base of food chains in terrestrial ecosystems, their productivity must necessarily influence all higher trophic levels. This is the basis for bottom-up regulation of food webs. However, higher trophic levels, if self-regulating, can impose top-down regulation on lower levels, or both bottom-up and top-down regulation can occur simultaneously (Sinclair et al. 2003). Regulation occurs when there is a density-dependent loss imposed on a population (Sinclair 1989). Strong evidence for top-down regulation comes from the removal of higher trophic levels resulting in a marked increase in prey populations or a reduction in prey if the predator population is experimentally increased. Second, compelling evidence for top-down regulation derives from evidence that mortality is largely or completely due to predation. Third, further evidence for a trophic cascade comes from indirect responses at the plant trophic level (e.g., increase or decline in growth, density) resulting from changes in predator numbers.

Evidence for bottom-up regulation is most powerful where density-dependent mortality is caused ultimately by lack of food. Second, evidence comes from density-dependent reduction in the instantaneous rate of increase in the absence of predation. Third, but less powerfully, evidence comes from predator removal experiments, in which there is little or no response in the prey population because the latter is regulated from below.

We present here evidence for both top-down and bottom-up processes, based on the aforementioned criteria, from a series of natural experiments in the Serengeti ecosystem resulting from perturbations, at different times, of the predator, herbivore, and plant trophic levels. First, the appearance of a viral disease, rinderpest, reduced herbivore numbers in the 1890s. Later, when the virus disappeared in the 1960s, it released herbivore numbers. Second, a predator removal took place in the 1980s, and comparisons of the effects of this removal could be made with simultaneous controls before and after the removals. Third, the trophic cascade that resulted from the rinderpest virus could be measured at the plant trophic level, and finally the effects on tree populations of the removal of the African elephant in the 1980s, due to poaching, could be compared with simultaneous undisturbed areas before and after the megaherbivore removals. A detailed account of these disturbances is reported in Sinclair et al. (2007, 2008). We compare these results with other areas in Africa and Asia.

TOP-DOWN REGULATION

Food webs can be thought of as modules of closely interacting species, and these modules are less closely connected to others. In the Serengeti system we see the large mammal community as one such module, and this is only loosely connected to one involving birds, insects, and plants, for example. Here we examine trophic cascades in the grassland mammal community, the grassland bird community, and the forest bird community.

The Small Ungulates

The strongest evidence for top-down processes affecting mammalian herbivores comes from situations in which predators have been removed and their prey display ecological release. An unplanned predator removal, largely of lions (*Panthera leo*), took place in northern Serengeti in the period 1980–1988 because of illegal hunting. Immediately adjacent to this area, on the Kenya side of the border, is the Masai Mara National Reserve, where predators were not removed, and so this area acted as a control. Population densities of small ungulates such as oribi (*Ourebia ourebi*), Thomson's gazelle (*Gazella thomsoni*), warthog (*Phacochoerus aethiopicus*), impala (*Aepyceros melampus*), and topi (*Damaliscus korrigum*) have been documented since the 1970s in both the predator removal and control areas (Figure 15.1). In all these species there was a major increase in density during the period of low lion numbers relative to the period before removal and to the period subsequently (1989–1998), when hunting ceased and predators returned. In contrast, no such changes took place in the adjacent

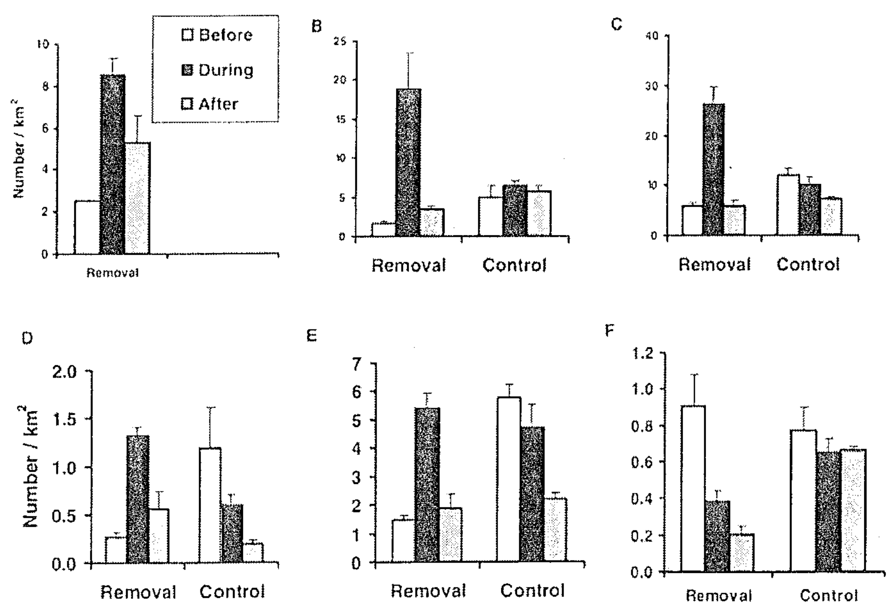

Figure 15.1. Density of ungulates in northern Serengeti where lions were removed in 1980–1988 (black bar) compared to preremoval (1967–1978) (open bar) and postremoval (1989–1998) (gray bar), and compared with the control in the Mara Reserve. **(a)** Oribi (not present in the control); **(b)** Thomson's gazelle; **(c)** impala; **(d)** warthog; **(e)** topi; **(f)** giraffe. Vertical bars = 1 *SE*. (From Sinclair et al. 2003)

control area. African buffalo had been removed by poaching some 6 years before the reduction in lion numbers. Furthermore, buffalo have remained absent both during the predator removal and after predators returned. Densities of smaller ungulates were similar in the 1970s, before predator removal and with high buffalo density, and in the 1990s after predators returned but with no buffalo present. Thus, the absence of buffalo did not explain the observed changes in other ungulates. These results provide compelling evidence for top-down effects (Sinclair et al. 2003).

More circumstantial evidence for trophic cascades in the mammal community comes from private reserves and ranches in southern Africa where predators have been removed. Wild ungulates have increased in number and are controlled by game ranching programs (Walker et al. 1987; Teer 1990). In contrast, where predators have been allowed to return on ranches in the Laikipia area of Kenya, populations of smaller ungulates have been reduced by predation (Georgiadis et al. 2007a, 2007b).

In Kruger Park, South Africa, predation was the dominant cause of mortality for small and medium-sized ungulates (Mills et al. 1995; Owen-Smith and Mills 2008). The creation of new water holes in the mid-twentieth century promoted the expansion of zebra (*Equus burchelli*) populations into new areas that, in turn, allowed lions to move in and drive down rare secondary prey, particularly roan antelope (*Hippotragus equinus*) and tsessebe (*Damaliscus lunatus*) (Harrington et al. 1999). Warthog (*Phacochoerus aethiopicus*) have also declined in numbers through intensified predation (Owen-Smith et al. 2005).

Top-down or bottom-up regulation of resident ungulates is determined by body size (Sinclair et al. 2003). Natural selection has pushed large ungulates to outgrow their predators, and predation is a minor component of adult mortality (Figure 15.2). However, below a certain threshold body size (about 150 kilograms body mass in Serengeti but likely to vary between ecosystems) there is a rapid switch from bottom-up to top-down regulation. As prey become smaller they are exposed to a greater number of predators until all adult mortality is caused by predation. The increased number of predators of small prey results from the food niches of small predators lying within those of larger predators (Sinclair et al. 2003; Radloff and du Toit 2004). Although the mode of preferred prey body size is different for each predator, the overlap in niche results in higher incidental predation of smaller prey compared with that of larger prey. This pattern of inclusive food niches for large mammal predators appears in both African and Asian savanna systems, such as at Nagarahole in southern India with tigers (*Panthera tigris*), leopards (*Panthera pardus*), and dhole (*Cuon alpinus*) (Karanth and Sunquist 1995). In essence, the size diversity of predators

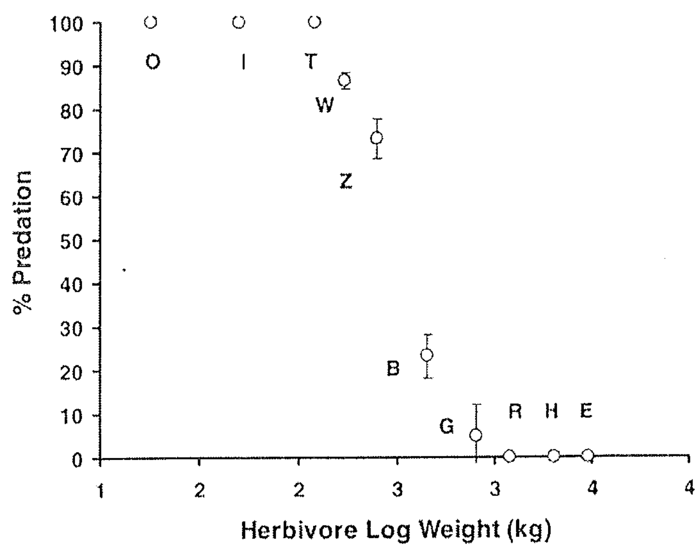

Figure 15.2. The proportion of adult mortality accounted for by predation relative to body mass in Serengeti. There is a threshold at about 150 kilograms where mortality switches from largely predation below to undernutrition above (from Sinclair et al. 2003). B = buffalo; E = African elephant; G = giraffe; H = hippo; I = impala; O = oribi; R = black rhino; T = topi; W = wildebeest; Z = zebra.

and prey results in both top-down and bottom-up processes occurring in the same system.

Overlap between dietary niches of predators is also likely to affect the response of prey to predator removal. Where the removal of one predator is compensated by an increase in another predator or predators of overlapping diet, we might expect prey release to be dampened or absent. Such is often the case in observations of mesopredator release, in which smaller predators increase in abundance and impact after the decline or extirpation of apex predators (Chapter 13, this volume). In such scenarios, the threshold prey body size that determines whether prey are bottom-up or top-down regulated should shift downward as smaller predators replace larger ones. This prediction is supported by observations of prey dynamics in altered wildlife communities or after extirpation and reintroduction of apex predators (e.g., gray wolves [*Canis lupus*] in the western United States; Chapter 9, this volume).

Impacts of Ungulates on Plants

The impact of ungulates on their plant prey has been documented for hundreds of years, most powerfully through the use of herbivore exclosures.

Recently, Pringle et al. (2007b) excluded ungulates from six *Acacia* savanna sites in Kenya for 5–9 years. Relative to control areas, there was a significant increase in tree densities but only a marginal increase in the herb layer cover. Associated with tree abundance was an increase in gecko and beetle numbers, suggesting the presence of strong indirect effects of ungulate predation on young trees.

In Serengeti, the most striking example of a trophic cascade reaching the plant level is the widespread increase in grass biomass that followed the collapse of wildebeest (*Connochaetes taurinus*) numbers in the 1890s as a result of disease outbreak (Sinclair 1979). This increase in vegetation biomass had two distinct consequences depending on habitat. On the eastern Serengeti plains, currently a shortgrass sward about 10 centimeters high, there was a change in structure that was observed at least in the 1930s–1950s (M. Leakey and A. Root, personal communication, 1977) with grass 50–70 centimeters high. A 10- by 10-meter grazing exclosure set up on these plains for 10 years generated a similar tallgrass sward in 1986 (personal observation). The change in grass biomass on the plains from shortgrass to tallgrass has several indirect cascading consequences. Among these changes were a major drop in dicot diversity from seventy species on grazed swards to fifteen species in ungrazed swards because grass, released from grazing, can outcompete small prostrate dicots for nutrients and light (Sinclair, unpublished data).

The second consequence of the lack of grazing during the 1890–1963 period occurred in the savanna habitats. During the dry season, wildebeest grazing maintains a grass biomass of about 700 (±150) kilograms per hectare and 10 centimeters in height. Without grazing this biomass is about 6,200 (*SE* ±380) kilograms per hectare (Figure 15.3) and provides fuel for widespread grass fires. Before the wildebeest increased in the 1960s, on average 80 percent of the northern Serengeti savanna burned each year (Norton-Griffiths 1979), whereas after wildebeest reached high numbers in 1977, the area burned dropped to below 20 percent (Sinclair et al. 2007). Although there was an initial increase in tree densities in 1890–1900 (because of the exodus of people because of rinderpest), burning increased after 1920 when people returned. Burning inhibits the regeneration of *Acacia* tree seedlings so that over the 50 years of widespread fires (1920–1970) there was a progressive reduction in savanna trees. When grazing impacts returned and burning was reduced after 1970, there was widespread regeneration of trees that formed, by the 2000s, a dense stand of trees (Sinclair et al. 2007). Further indirect consequences of this trophic cascade are now being documented on birds, rodents, and insects.

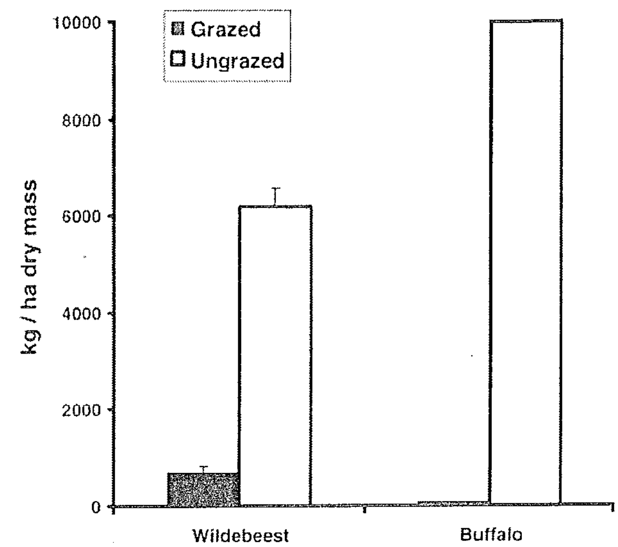

Figure 15.3. The impact of wildebeest grazing on the biomass of grass in the savanna of Serengeti and African buffalo grazing on swards of montane grassland at Mt. Meru, Tanzania, both relative to plots protected from grazing, showing top-down impacts. (A. Sinclair unpublished)

Impacts of Birds on Insects

Empirical evidence exists for top-down impacts of birds on insects. Of the 640 species of birds in the Serengeti, some 104 are vertebrate feeders, many on birds, and 343 are insectivores, compared to 115 seed or fruit feeders. Thus, the dominant food chain in terms of avian species and their prey is raptors ↔ bird insectivores ↔ insects.

Insight on the role of top-down and bottom-up regulation of insectivorous birds can be gained in areas where grazing and burning act as natural experimental removals of the grass level. A bottom-up process would predict lower insect biomass and consequently lower insectivorous bird biomass from such grass removals. In contrast, a top-down process would predict no decline in bird populations. Nkwabi (2007) compared burnt and grazed areas with matched undisturbed sites. Insect biomass decreased on disturbed relative to undisturbed sites (Figure 15.4a), but bird numbers increased (Figure 15.4b), and the bird community changed. The inference is that the change in plant structure facilitated the ability of birds to find prey (i.e., improved their functional response), and so birds at least contributed to the lower insect biomass, a top-down effect.

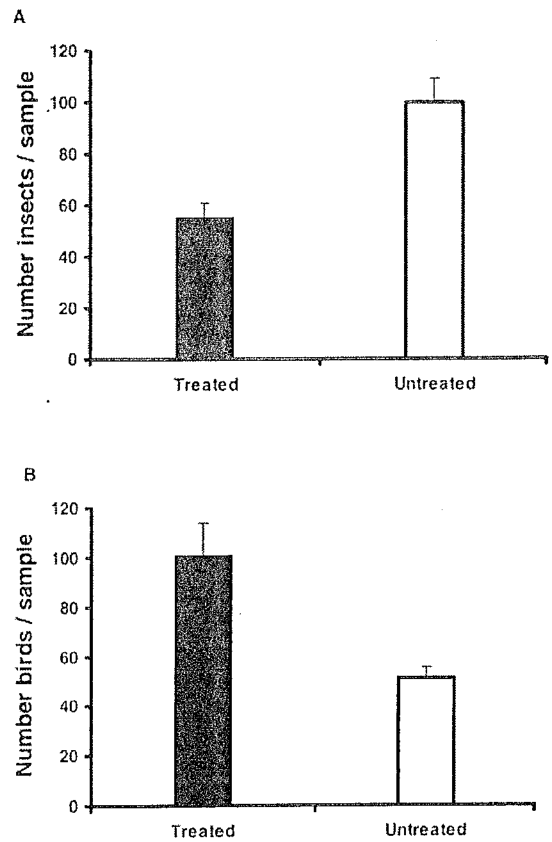

Figure 15.4. Top-down impacts of birds on insects measured from a plant biomass removal. **(a)** The mean (±1 *SE*) number of insects per sample from pitfall, tray traps, and sweepnets combined, on burnt or grazed plots (treated) compared with ungrazed or unburnt plots (untreated). **(b)** The mean number of ground- or grass-living insectivorous birds on the same sites counted over 10-minute intervals through the dry season after grazing or burning. (Data from Nkwabi 2007)

Few other studies have examined the effects of burning and grazing on bird populations in Africa (Parr and Chown 2003). In Kenya, burning had little effect on grassland bird abundance (O'Reilly et al. 2006), whereas in South Africa grazed areas resulted in an increase in some ground-living francolin (*Francolinus* sp.) species (Jansen et al. 1999), both results suggesting a role for top-down processes.

Impacts of Birds on Forest Communities

A small but growing body of research has examined the top-down effect of birds on forest dynamics, specifically seed dispersal and regeneration (e.g., Pejchar et al. 2008). Evergreen closed-canopy forest grows along the major rivers of Serengeti. On the Mara River, regeneration of forest occurs through seedlings growing up underneath the closed canopy. In contrast, in light gaps where the canopy has been opened through disturbance, grass invades and tree seedlings are excluded. In addition, seedlings are also absent in such open canopy forest, even under canopy where grass does not occur (Sharam 2005). Fire and browsing by elephants act as natural experimental removers of the canopy, leaving some riverine patches with open canopy and others closed. Sharam et al. (2009) compared forest patches with different degrees of openness. Obligate forest bird species were lost as the canopy opened up, with frugivores being more adversely affected than insectivores. Frugivores consume tree fruits and leave the seeds (without pericarp) on the ground, where they could germinate. If fruits are not eaten they eventually fall to the ground with pericarp still present. Bruchid beetles attack seeds with pericarp, and these fail to germinate. Seeds without pericarp are attacked less, and germination is high. Thus, in open canopy forest, without frugivores, insect attack is higher, seedling density declines, and the forest canopy continues to open until all trees have disappeared, leaving only shrubs. This positive feedback unraveling of the forest has been tracked in one patch since 1966 (Sharam et al. 2009). In essence, birds depress beetles indirectly, which promotes seedling regeneration and a stable closed-canopy forest, a top-down cascade.

BOTTOM-UP REGULATION

Several conditions allow bottom-up regulation of the food web modules. One condition depends on body size, particularly in mammal herbivores that have outgrown their predators. Another condition is that of the behavior of the herbivores through both migration and group living. A third condition depends on position in the food web; top predators are necessarily dependent on food supply, but the effects of resources are modified by whether the predators live in groups or are lone hunters.

The Megaherbivores

Between the 1890s and 1964, the African buffalo (*Syncerus caffer*) population in Serengeti suffered severe mortality in the first year age group due to rinderpest (Sinclair 1977; Dobson 1995). The disease disappeared in 1964, as an ancillary benefit of a vaccination campaign on cattle. Buffalo, thus released from disease, increased in number until 1976, when they began to level out as a result of lack of food, whereupon the instantaneous rate of increase declined (Figure 15.5a). Reduced population growth resulted largely from density-dependent mortality of adults (Figure 15.5b). Analysis of the carcasses showed that undernutrition accounted for some 75 percent of the mortality. Predation by lions accounted for the other 25 percent, but most of this involved prey that were already in a

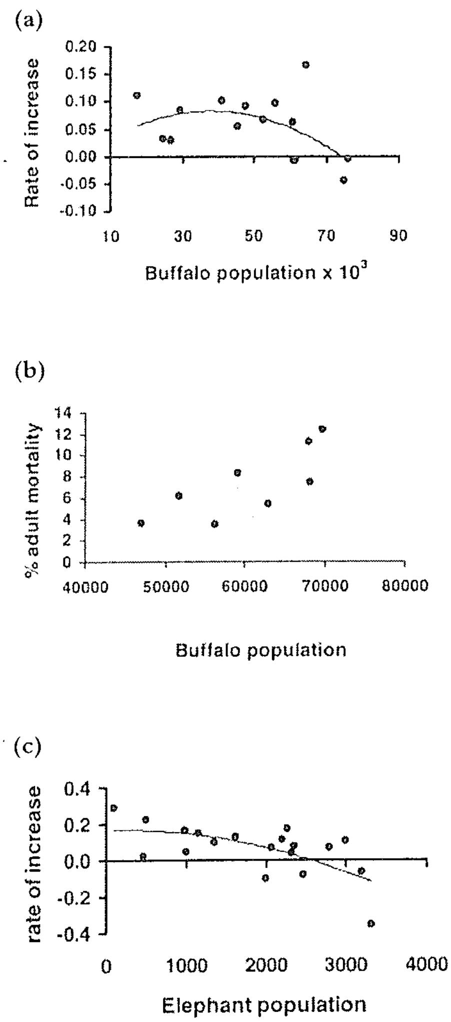

Figure 15.5. Evidence for bottom-up processes in resident megaherbivores. **(a)** The instantaneous rate of increase of the Serengeti buffalo population after reductions by rinderpest or poaching. **(b)** Density-dependent percentage adult mortality of buffalo due to undernutrition (from Sinclair 1977). **(c)** The instantaneous rate of increase of the Serengeti elephant population due to both immigration and births after reductions by poaching. (Data from Sinclair 2003 and unpublished)

state of undernutrition, as was judged objectively by inspection of the marrow in leg bones. In ungulates, fat is stored to cover periods of food limitation, the main stores being in the gut mesentery and the bone marrow. The last fat to be used lies in the leg bones, which after it is depleted leaves a translucent gelatinous marrow clearly visible in dead animals (Hanks 1981; Sinclair and Arcese 1995).

Another form of evidence for bottom-up regulation in buffalo allows a generalization that applies across eastern Africa. Buffalo eat grass only, and the best predictor for the biomass of grass is annual rainfall. Densities of buffalo close to their equilibrium number are significantly related to rainfall in twelve East African protected areas (Sinclair 1977). The interpretation is that rainfall, acting through the food supply, determines the equilibrium level of buffalo populations (Sinclair 1977). This observation can be generalized across Africa where ungulate biomass and productivity are positively related to their food supply (Coe et al. 1976; Fritz and Duncan 1993).

African elephant populations also demonstrate bottom-up regulation. Evidence comes from the subsequent population responses to the removal of elephants by humans. In Serengeti this has occurred twice. The first took place in the 1880s, when the ivory trade effectively removed all elephants from Serengeti until the 1950s. The second occurred in the 1977–1988 period, when illegal hunting was rampant in the system (Sinclair et al. 2008). After each population reduction, elephants have increased, showing a density-dependent slowing in the rate of increase (Figure 15.5c). Similarly, in Hwange National Park, Zimbabwe, elephants were released from culling in 1986, and subsequent population growth rates were negatively related to population density (Chamaille-Jammes et al. 2008; Sinclair et al. 2008). In Kruger National Park, South Africa, continuous culling of elephants from 1965 to 2000 (Whyte et al. 2003) can be regarded as experimental removals. Again, a density-dependent change in the rate of increase subsequent to each removal was exhibited by the population (Sinclair and Metzger 2009); reductions to lower density resulted in faster rates of increase.

Regulation of elephant numbers takes place through lack of food in the dry season, and predators are not involved. The mechanism was seen most clearly in Tsavo National Park, Kenya. Populations there were increasing after the imposition of protection from hunting in the 1950s. Their food in the dry season consisted of shrubs and trees within reach of water supplies, because water is an essential resource. As numbers increased they first consumed trees near water, then progressively further away until they were just able to reach their food. In 1971 a drought resulted in insufficient food within reach of water, and a large proportion (perhaps 30 percent) died of starvation (Corfield 1973; Myers 1973; Croze et al. 1981). The spatial distribution of elephants relative to food within reach of water supplies was the important feature regulating elephants in Hwange Park, Zimbabwe (Chamaille-Jammes et al. 2008). Evidence for food regulation of megaherbivores is also reported for white rhino (*Ceratotherium simum*) in South Africa (Owen-Smith 1981, 1988) and for elephants and hippopotamus in Uganda (Laws et al. 1975; Eltringham 1980).

The predator removal experiment in northern Serengeti in the 1980s (described earlier) detected no difference in the population trend of giraffe (*Giraffa camelopardalis*) in the removal area compared with that in the nonremoval area. Giraffe are regulated through food supply both in Serengeti (Pellew 1983) and in Laikipia, Kenya (Georgiadis et al. 2007a).

In summary, mammal herbivores over 400 kilograms (the size of buffalo or larger) in Serengeti suffer little or no predation as adults and are regulated ultimately through food supply. In other areas such as Kruger, the larger ungulates are also food limited (Owen-Smith 1990; Owen-Smith and Ogutu 2003). However, studies are showing that both disease (Cleaveland et al. 2008) and predation (Sinclair and Arcese 1995; Owen-Smith et al. 2005; Owen-Smith and Mills 2008) can act synergistically with food scarcity by expediting mortality. This increases the sensitivity of herbivore populations to fluctuations in bottom-up processes and provides stability to the system.

The Migrant Ungulates

Like the buffalo, the calves of migrant wildebeest of Serengeti experienced high mortality from rinderpest before 1963. As in buffalo, the disease died out, but in 1962, and the population increased sixfold until 1977. At that time it leveled out and has remained between 1.2 and 1.4 million animals since then, with the exception of 1993, when 25 percent died due to the most severe drought yet recorded (Mduma et al. 1999).

Because of the release from disease mortality, the wildebeest population showed density-dependent changes in the rate of increase (Sinclair and Krebs 2002). Adult mortality showed two trends (Figure 15.6a), initially an inverse density-dependent phase in which mortality was largely caused by predation, and a later phase in which mortality was strongly density-dependent. The later phase was caused by an increasing proportion of starving animals as density relative to food increased (Figure 15.6b) and per capita food supply declined (Figure 15.6c), resulting in lower body fat reserves (Sinclair et al. 1985; Mduma et al. 1999).

Migration is an adaptation to access ephemeral but highly nutritious food

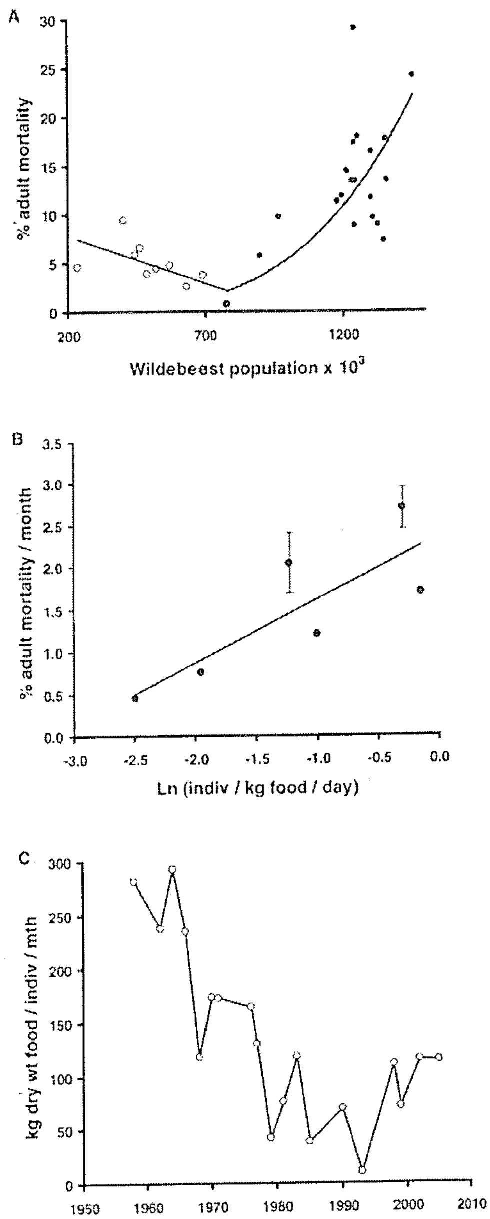

Figure 15.6. Evidence for bottom-up processes in migrant wildebeest. **(a)** The percentage adult mortality relative to population size. At low numbers mortality was largely inverse density-dependent predation, as explained in the text (open circles); at higher numbers density-dependent mortality was caused largely by undernutrition (closed circles) (data from Mduma et al. 1999). **(b)** The percentage adult mortality in the dry season is related to the density of animals with respect to food supply (from Sinclair et al. 1985). **(c)** Per capita food supply has declined over time as the population increased and leveled out. (Data from Mduma et al. 1999 and unpublished data)

supplies, a feature common to most if not all migrating ungulates, whales, and birds. In the case of migrating wildebeest, these ephemeral foods occur on the shortgrass plains where the plants are very high in nutrients but are green for only a few months each year. The wildebeest move to these shortgrass plains while the grass is still green but then must return to the tallgrass savanna when the plains dry out. The extra food on the plains provides for the growth of fetuses and lactation and results in a much higher density of animals than is observed in sedentary populations; we can compare this migratory population with a sedentary population in western Serengeti. Fryxell and Sinclair (1988a) have produced a model to show how migrant animals can escape from top-down effects of predation and so become food regulated. Similar tracking of ephemeral resources by migrant ungulates is seen in white-eared kob (*Kobus kob*) of Sudan (Fryxell and Sinclair 1988b), wildebeest, springbok (*Antidorcas marsupialis*), and gemsbok (*Oryx gazella*) in southern Africa (Viljoen 1993).

However, the migrant zebra populations of Serengeti and southern Africa are an exception. They appear to be top-down regulated (Grange et al. 2004). Although the mechanism is not entirely clear, one possibility is that that they do not all migrate; a portion of the population does migrate, but the rest are spread across the ecosystem, where they are exposed, like other residents, to high predation rates. Combined with their low reproductive rates, this predation is sufficient to hold them down.

The Major Predators

Lion and hyena (*Crocuta crocuta*) populations, the main predators on the Serengeti plains, have also increased as their prey increased, particularly the wildebeest population (Van Orsdol et al. 1985; Hanby et al. 1995; Scheel and Packer 1995; Packer et al. 2005). Lion densities are correlated with prey availability in the "poor season," when migrant populations are absent. However, migrant wildebeest leave behind them sick and aged members, which do not migrate and become part of the resident prey. As wildebeest increased in number and became resource limited, a greater number of stragglers became available, thus providing a bottom-up enhancement for the major predators.

In general, this conclusion applies elsewhere in Africa and India. East (1984) showed that the biomass of the major predators—lion, spotted hyena, cheetah, and leopard—was positively correlated with the biomass of their main ungulate prey over savanna Africa. Similarly in eleven savanna and woodland reserves of India the density of tigers is positively related to the density of their ungulate prey (Karanth and Nichols 1998; Karanth et al. 2004), which is evidence for bottom-up regulation.

RECIPROCAL TROPHIC INTERACTIONS

Although large resident ungulates such as buffalo and elephant are bottom-up regulated, they can also have reciprocal top-down impacts on plants, but such impacts depend on the season when they occur. Thus, buffalo in the Serengeti are food limited in the dry season when grasses are dormant. Even total removal of the aboveground dry material has no impact on the viability of the grass, and consequently there is no impact on either plant composition or productivity. The same argument applies with wildebeest grazing in the dry season. In short, there is no top-down effect on plants when plants protect their growing points and storage organs in the soil during the dormant season.

A different situation prevails when herbivores feed on dicots or on green monocots during the period of food scarcity. Buffalo occur on Mt. Meru, some 300 kilometers east of Serengeti, where they are the only major grazer and have no natural predators. Continuous grazing on year-round green swards at 2,000 meters altitude maintains a green shortgrass sward (less than 10 centimeters height) of 72 (*SE* ±10.5) kilograms per hectare of prostrate grasses and dicots with a stable species composition (Figure 15.3). Tall tussock grasses (70 centimeters) replaced the low sward at a biomass of 10,000 kilograms per hectare in exclosures within 5 years (Sinclair 1977). Similarly, on the shortgrass plains of Serengeti, the grazing impact of wildebeest takes place during the growing season and determines plant species composition, structure, and productivity. In these cases, the removal of herbivores releases the vegetation from top-down forces and permits large increases in plant biomass. Species that feed on dicots, such as giraffe, are bottom-up limited but also have structuring effects on their own food supply by inhibiting the escape of small trees into the adult stages and changing species composition (Pellew 1983; Bond and Loffell 2001; Scholes et al. 2003).

Elephant, white rhinos, and hippopotamus also have reciprocal top-down impacts on plants, as has been well documented in many areas such as Uganda, Kenya, Tanzania, Botswana, Zimbabwe, and South Africa (Laws 1970; Laws et al. 1975; Norton-Griffiths 1979; Eltringham 1980; Owen-Smith 1988; Cumming et al. 1997; Eckhardt et al. 2000; Scholes et al. 2003; Chamaille-Jammes et al. 2008). Both white rhino and hippopotamus convert tall tussock grasslands into shortgrass communities. Top-down effects occur with African elephants when they feed on trees year-round and have no alternative food sources, as in Tsavo National Park, Kenya. Asian elephants (*Elephas maximus*) can also affect vegetation in savanna or woodland areas, such as Satyamangalam, Bandipur, and

Kaziranga in India; Chitawan, Nepal; and Wilpattu and Gal Oya, Sri Lanka (Sukumar 1988).

Evidence implicating elephants in trophic cascades derives from situations in which they were completely removed during the ivory trade of the mid-1800s, as in Chobe Park, Botswana; Kruger, South Africa; and Tsavo, Kenya (Patterson 1907; Myers 1973; Whyte et al. 2003; Skarpe et al. 2004). In the absence of elephants, extensive tree and shrub communities developed, especially along riverbanks. When elephants returned after the 1950s, the plant composition changed and the vegetation became more open (often with aesthetic, ethical, and conservation repercussions). In another demonstration, woody vegetation experienced strong recruitment in Tsavo after 6,000 elephants died of starvation in 1971 (Croze et al. 1981), and in Chobe broad-leaved woodlands originated only during episodes of regeneration when browsing by elephants and impala was low (Moe et al. 2009).

Reciprocal interactions between carnivores and their prey have been documented in Kruger Park, South Africa. Predation was synergistic with the bottom-up effects of nutrition in larger ungulates, especially for the larger buffalo and giraffe (Owen-Smith and Ogutu 2003), as occurs in Serengeti.

MULTIPLE STATES: TOP-DOWN OR BOTTOM-UP

We have also recorded a situation in Serengeti where top-down and bottom-up processes involving elephants and plants alternate as two different states (Dublin et al. 1990; Sinclair and Krebs 2002). This situation was elucidated by two different disturbances to the system. First, during a period when there was extensive *Acacia* tree canopy (more than 30 percent cover), monitoring of tree mortality attributable to elephants showed that elephants were unable to reduce the tree population. However, both monitoring of burning and experiments with fire demonstrated that widespread burning over a period of some 50 years (1930s–1970s) reduced tree densities parkwide (Norton-Griffiths 1979; Dublin et al. 1990; Sinclair et al. 2007), effects that have been recorded elsewhere in savannas (Chapter 16, this volume). In the far northern part of the ecosystem, the Mara Reserve of Kenya, less than 1 percent cover remained by 1980. In this area elephants changed their feeding from large trees to seedlings, often less than 15 centimeters high (Dublin 1986), and they were so efficient at weeding them out of the grass sward that they prevented tree regeneration. This conclusion was derived from experimental elephant exclosures and marked plants (Dublin et al. 1990). Thus, elephants were able to impose top-down regulation on the tree population, but only once trees had been reduced to very low numbers. This is the classic Type III functional response of a predator (elephants) regulating prey at low densities but not at high densities (Pech et al. 1992; Sinclair et al. 1998).

The second disturbance occurred in the 1980s when illegal hunting for ivory removed 80 percent of elephants in Serengeti but left untouched the elephants in the Mara Reserve (Sinclair et al. 2007). The consequence of elephant removal was the resurgence of *Acacia* seedlings in Serengeti but not in the Mara. Thus, in summary, there are two possible states with the same density of elephants as now occurs in the ecosystem: one with trees and elephants by bottom-up processes and, in another part of the system, a grassland with elephants imposing a top-down restraint on tree regeneration.

Management interventions carried out in Kruger National Park (South Africa) also hint at multiple states. Smuts (1978) reported that when wildebeest were in high numbers, lion fed on them but did not regulate them. However, when wildebeest were experimentally reduced in number, their diminished grazing allowed tall grass to grow, which improved the functional response of lions. The combination of lower prey numbers and greater capture rates allowed lions to reduce wildebeest numbers even further.

SYNTHESIS: INTERACTIONS OF BOTTOM-UP AND TOP-DOWN FOOD CHAINS

Trophic relationships in Serengeti are complicated by the presence of both migratory and sedentary herbivores and by the presence of herbivore species regulated from the top by predators and others regulated from the bottom by forage availability. Herding greatly lowers the per capita predation rate on wildebeest and other species that associate with them because it can bring hundreds of thousands of prey into the territory of a single lion pride and saturate its resource needs. At the same time, the vast concentration of prey contained in herds alleviates predation pressure on resident herbivores, allowing them a respite in which to reproduce. Thus, different components of the system interact in ways that confer stability to the whole (Figure 15.7). Several observations support this conclusion.

First, there is a bottom-up current of regulation from grass to wildebeest and wildebeest to lions, as was demonstrated when wildebeest were recovering from rinderpest. A concurrent increase in lions demonstrated that lion populations are supported by migrant herbivores. In turn, lions have a top-down

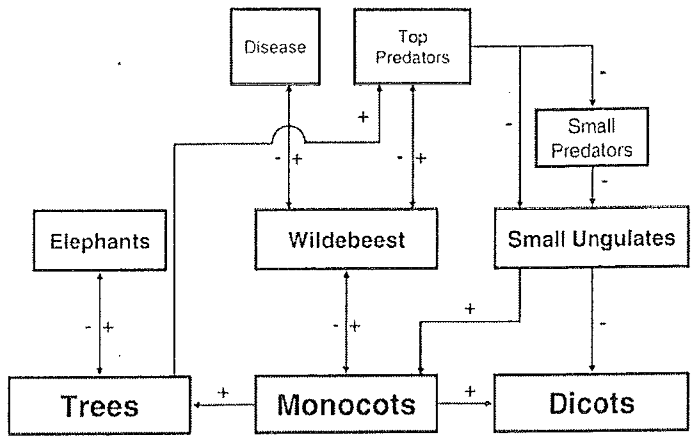

Figure 15.7. Flow diagram of trophic processes in Serengeti showing reciprocal interactions and the connection between bottom-up regulation of migrant wildebeest and top-down regulation of resident ungulates.

regulating effect on both smaller predator species, such as cheetah (*Acinonyx jubatus*) (Laurenson 1995), and smaller ungulates. Consequently, small ungulates have little impact on their food resources in Serengeti. In short, the bottom-up chain intensifies the top-down chain.

Second, the reciprocal impact of wildebeest on their own food supply has the indirect effect of promoting and maintaining both the tree population in savanna habitats and the dicot communities on the plains. In the savanna, trees then regulate elephant numbers, which in turn have a reciprocal effect on tree regeneration, as was demonstrated by elephant removal in Serengeti (Sinclair et al. 2007).

Third, the increase in tree density as a result of the recovery of wildebeest improved the ability of lions to catch their prey in savanna habitats. Since the leveling-out of wildebeest numbers in 1977, lion numbers have continued to increase, a fact attributed to greater success of lions in catching their prey (Packer et al. 2005). Thickets of regenerating trees provide cover from which lions can ambush prey (Hopcraft et al. 2005). In summary, lion numbers have increased whereas resident and migrant prey have not, which is further evidence of a top-down regulation of resident prey by predators.

Fourth, the functional responses of group-living predators depending on group-living prey provide strong stabilizing effects on the trophic cascade (Fryxell et al. 2007). Herding by prey reduces the search efficiency of predators because there are large areas of the habitat with no prey through which the predators have to move to reach a herd. Social behavior of prey therefore reduces the frequency with which predators encounter prey (Cosner et al. 1999; Nachman 2006). Grouping by predators limits search efficiency to a level similar to that of a solitary predator because they operate largely as a single entity. Although cooperation may compensate by improving the chance of capture, especially for large prey such as African buffalo, this compensation is small (Packer and Ruttan 1988). Most individual lions refrain from contributing to group hunts except when pursuing buffalo, which are inaccessible to solitary individuals or small groups (Scheel and Packer 1991). In summary, group formation and seasonal migration in ungulates are behavioral mechanisms that contribute substantially to the stability of top-down interactions in Serengeti.

Similar interactions of bottom-up processes supplementing countercurrent top-down pathways are reported for wild ungulates in the Laikipia district of Kenya: The dominant grazers (zebra) and browsers (giraffe) are regulated through food supply, but they support large predators that regulate several other smaller ungulate species (Georgiadis et al. 2007a, 2007b; Chapter 18, this volume).

The savanna systems of Africa and Asia are dominated by ungulates. The larger species are regulated by their food supplies, and predator populations are in turn determined by ungulate densities, a bottom-up process. However, there are reciprocal top-down processes through which predators affect the numbers of medium and small ungulates. The Serengeti ecosystem is an example of a migratory system embedded in a community of resident species. This has resulted in a complex interaction of a bottom-up process supplementing a top-down trophic cascade. We have elucidated these regulatory mechanisms in the large mammal community through a series of perturbations to producer, consumer, and predator trophic levels. First, bottom-up processes regulate the megaherbivores, a feature also observed in many other savanna systems in Africa. Second, bottom-up processes usually regulate migrant populations, in this case wildebeest, a feature also observed in other migration systems. Third, top predators are supported by these migrant populations, and these predators then impose a top-down regulation on both other predators and small resident ungulates. Thus, not only are both types of food chain present, but they influence each other. Fourth, megaherbivores such as elephants also have a reciprocal top-down effect on the vegetation, changing its structure and species composition, a feature observed widely in Africa. Finally, although elephants are always bottom-up regulated, their top-down impacts are determined by the density of trees; only at low tree density do they have top-down effects. This results in multiple states in which elephants, at the same density, are merely responding to their food supplies and savanna prevails, or they impose top-down regulation on trees and grassland. Therefore, the density of trees determines whether elephants can impose top-down regulation on trees.

CONCLUSIONS

Serengeti is unique and invaluable for the insights it provides for the understanding of how natural systems work. It is one of the last places on the planet where an intact system of megafauna and migratory ungulates survives intact. It illustrates the richness and complexity of trophic interactions that are the norm in the absence of anthropogenic effects. At one time the entire world supported megafauna, and much of it supported migratory ungulates before humans spread around the earth and exterminated most large animals. Animal communities throughout most of evolutionary history must have been stabilized by dynamics similar to those in Serengeti. The residual systems that are all we have nearly everywhere else are anthropogenic artifacts.

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