
Long-Term Ecosystem Dynamics in the Serengeti: Lessons for Conservation

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Abstract: *Data from long-term ecological studies further understanding of ecosystem dynamics and can guide evidence-based management. In a quasi-natural experiment we examined long-term monitoring data on different components of the Serengeti-Mara Ecosystem to trace the effects of disturbances and thus to elucidate cause-and-effect connections between them. The long-term data illustrated the role of food limitation in population regulation in mammals, particularly in migratory wildebeest and nonmigratory buffalo. Predation limited populations of smaller resident ungulates and small carnivores. Abiotic events, such as droughts and floods, created disturbances that affected survivorship of ungulates and birds. Such disturbances showed feedbacks between biotic and abiotic realms. Interactions between elephants and their food allowed savanna and grassland communities to co-occur. With increased woodland vegetation, predators' capture of prey increased. Anthropogenic disturbances had direct (hunting) and indirect (transfer of disease to wildlife) effects. Slow and rapid changes and multiple ecosystem states became apparent only over several decades and involved events at different spatial scales. Conservation efforts should accommodate both infrequent and unpredictable events and long-term trends. Management should plan on the time scale of those events and should not aim to maintain the status quo. Systems can be self-regulating through food availability and predator-prey interactions; thus, culling may not be required. Ecosystems can occur in multiple states; thus, there may be no a priori need to maintain one natural state. Finally, conservation efforts outside protected areas must distinguish between natural change and direct human-induced change. Protected areas can act as ecological baselines in which human-induced change is kept to a minimum*

Keywords: anthropogenic disturbance, ecological baselines, long-term monitoring, multiple ecosystem states, natural disturbance, protected areas, rinderpest, Serengeti

Dinámica del Ecosistema a Largo Plazo en el Serengeti: Lecciones para la Conservación

Resumen: *Los datos de estudios ecológicos de largo plazo favorecen el entendimiento de la dinámica del ecosistema. En un experimento cuasi natural, examinamos los datos de monitoreo de largo plazo de diferentes componentes del Ecosistema Serengeti-Mara para rastrear los efectos de perturbaciones y por lo tanto dilucidar conexiones causa-efecto entre ellos. Los datos de largo plazo mostraron el papel de la limitación de alimento en la regulación poblacional de mamíferos, particularmente en ñus migratorios y búfalos no migratorios. La depredación limitó a las poblaciones de ungulados menores residentes y carnívoros pequeños. Los eventos abióticos, como sequías e inundaciones, crearon perturbaciones que afectaron la supervivencia de ungulados y aves. Tales perturbaciones mostraron realimentaciones entre las esferas biótica y abiótica.*

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Las interacciones entre elefantes y su alimento permitieron la co-ocurrencia de comunidades de sabana y pastizal. Con el incremento de la vegetación leñosa, aumentó la captura de presas por los depredadores. Las perturbaciones antropogénicas tuvieron efectos directos (cacería) e indirectos (transferencia de enfermedades a la vida silvestre). Los cambios lentos y rápidos y los estados múltiples del ecosistema se hicieron aparentes solo después de varias décadas e involucraron eventos en diferentes escalas espaciales. Los esfuerzos de conservación deben acomodar tanto a eventos poco frecuentes como eventos impredecibles, así como las tendencias a largo plazo. La gestión debería planificar sobre la escala de tiempo de esos eventos y no debería tratar de mantener el status quo. Los sistemas pueden ser auto regulables por medio de la disponibilidad de alimento y las interacciones depredador - presa; por lo tanto, puede que no se requiera la caza selectiva. Los ecosistemas pueden ocurrir en estados múltiples; por lo tanto, a priori no hay necesidad de mantener un estado natural. Finalmente, los esfuerzos de conservación fuera de las áreas protegidas deben distinguir entre cambio natural y cambio inducido directamente por humanos. Las áreas protegidas pueden fungir como bases ecológicas donde los cambios inducidos por humanos son mantenidos al mínimo.

Palabras Clave: áreas protegidas, bases ecológicas, estados múltiples del ecosistema, monitoreo de largo plazo, perturbación antropogénica, perturbación natural, peste bovina, Serengeti

Introduction

The Serengeti-Mara Ecosystem (SME) in East Africa has been the subject of ecological study since the 1950s (Sinclair & Norton-Griffiths 1979; Sinclair & Arcese 1995). Like other long-term studies in protected areas such as Yellowstone National Park (United States; Keiter & Boyce 1991; National Research Council 2002; Biel 2004) and Kruger National Park, South Africa (du Toit et al. 2003), the information is being used for conservation and ecosystem management (Woodley 1997). We reviewed the insights that we obtained from natural and anthropogenic disturbances and examined the possible conservation applications of this long-term ecological record.

The SME is in the East African *Acacia* savanna zone (1°15' to 3°30'S, 34° to 36°E) adjacent to Lake Victoria. The majority is in Tanzania, but the northern part is in Kenya as the Masai Mara National Reserve (MMNR). The area is recognized as a World Heritage Site by UNESCO because of its large migratory ungulate populations, high diversity of large mammals and birds, prehistory sites at Laetoli and Olduvai, and representation of the tropical upland Plains-Savanna biome.

The first studies took place in the 1950s and related to the realignment of boundaries of the Serengeti National Park (SNP) and the Ngorongoro Conservation Area (NCA; Pearsall 1957; Brooks 1961; Anderson & Talbot 1965). An effort to document the ecosystem by John Owen resulted in the first systematic censuses of large ungulates in 1958 (Grzimek & Grzimek 1960a, 1960b; Stewart & Talbot 1962). Thus began a tradition of aerial censuses that continues today. Studies of the ecosystem expanded in the 1960s with the advent of the Serengeti Research Institute, when information on grasslands, woodlands, carnivores, and other groups became available. Subsequently, data gathering was intermittent and determined by the length of projects funded externally and political changes internally. In particular, there was a dearth

of information during 1977–1986, when the Tanzania-Kenya border was closed. Political and funding stability after 1986 allowed for an expansion of studies, including the ongoing Serengeti Biodiversity Program.

The most important factor that has contributed to our understanding of this ecosystem is the serendipitous appearance of disturbances. These have provided the conditions necessary to interpret the cause and effect linkages within the system.

Study Area

The SME covers some 25,000 km². The southeastern area lies in the rain shadow of the Ngorongoro highlands and is composed of shortgrass treeless plains with abundant small dicots. Soils are high in nutrients, overlying a shallow calcareous hardpan. A gradient of soil depth north-westward across the plains results in changes in the herbaceous community and taller grass. Some 70 km west, *Acacia* woodlands appear suddenly and stretch west to Lake Victoria and north to the Loita Plains, north of the MMNR. The 16 *Acacia* species vary over this range, their distribution determined by edaphic conditions and soil depth. Near Lake Victoria there are flood plains developed from ancient lakebeds. In the far northwest, *Acacia* woodlands are replaced by broadleaved *Terminalia-Combretum* woodlands, determined by a change in geology. This area has the highest rainfall in the system and forms a refuge for the migrating ungulates at the end of the dry season.

Disappearance of Rinderpest

The most significant perturbation of the ecosystem that we have observed has been the removal of the viral disea-

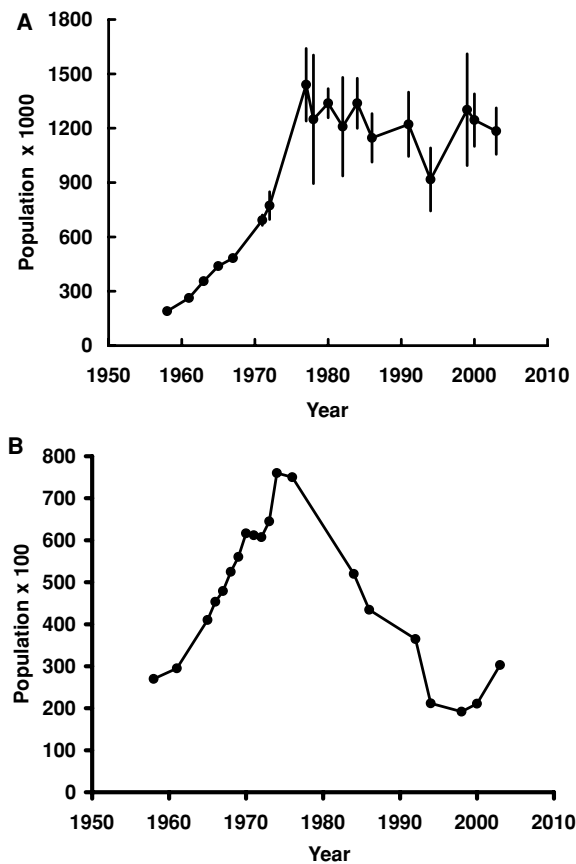


Figure 1. Changes in the populations of (a) migratory wildebeest (data in Mduma et al. 1999; Mduma & Hopcraft 2007; S.A.R.M., unpublished) and (b) African buffalo (data from Sinclair 1977; Dublin et al. 1990; A.R.E.S. & S.A.R.M., unpublished) over time.

se, rinderpest, an exotic that caused heavy mortality of some ruminants, particularly wildebeest (*Connochaetes taurinus*) and buffalo (*Syncerus caffer*). Rinderpest entered Africa via Ethiopia and Sudan in 1890, spread to the Cape by 1896, and created a panzootic that removed 95% of cattle, buffalo, and related species. Epizootics reappeared at intervals of 10–20 years until the 1950s when a cattle vaccination campaign surrounding Serengeti resulted in the virus disappearing from the wildlife (Sinclair 1977, 1979; Plowright 1982). After 1964 rinderpest was absent until 1982, when a mild form of the disease was found in buffalo, but not wildebeest (Rossiter et al. 1983), that had no detectable population affects (Dublin et al. 1990a). It is still absent from the system.

Survivorship of first-year juvenile wildebeest and buffalo doubled after rinderpest disappeared. Both populations increased rapidly until 1977 (Figs. 1a–b). Density-dependent mortality, particularly in old adults, stabilized both populations. This stability has been maintained in wildebeest to the present. In buffalo density dependence stabilized the population by the mid 1970s, but subse-

quent events related to poaching obscured this process until recently (see below). The cause of the density-dependent mortality was a progressive decrease in per capita green food during the dry season (Sinclair 1977; Sinclair et al. 1985; Mduma et al. 1999).

Identifying density-dependent mechanisms and their causes can best be achieved when populations are displaced from their potential equilibria by perturbations of known cause, either as deliberate experiments or unplanned natural experiments (Sinclair 1989). The rinderpest removal was of the latter type, and the insights that lead from it were fundamental for conservation and management. It led to the conclusion that populations, and hence communities, that are intact functioning ecosystems could be self-stabilizing so that management interference is not obligatory. Up to the 1970s managers assumed that interference by culling was required to prevent populations from increasing, an assumption that underlays the preemptive culling of elk (*Cervus elaphus*) in Yellowstone National Park (Houston 1982) and elephant (*Loxodonta africana*) in Zimbabwe (Anderson & Walker 1974) and Uganda (Laws et al. 1975) and that was the basis for plans to cull elephants in Tsavo National Park, Kenya, and elsewhere (Laws 1969; Jewell et al. 1981; Owen-Smith 1983).

Trends in Abiotic Factors

The major abiotic factors affecting the Serengeti ecosystem are fire and rainfall. Grass fires have dominated African savanna landscapes for hundreds of millennia (Bird & Cali 1998) and plants are fire tolerant. The savanna plant community is a fire disclimax that has been shaped by the frequency of burns (Frost & Robertson 1987). Although in Kruger lightning causes some 20% of fires (du Toit et al. 2003), in Serengeti fire is caused by humans; no lightning-caused fires have been recorded. The probability that grass fires will spread is determined by the amount of dry grass fuel and grass moisture (Stronach 1989), and fires occur only in the dry season, typically July–October. Records of the extent of burns during the dry season, documented by aerial reconnaissance, show a steady decline in the area burned from the early 1960s to the 1980s (Norton-Griffiths 1979; A.R.E.S., unpublished data). The few recent records that exist indicate that the extent of fire in the north and center of Serengeti remains low. These trends are related to the increase in wildebeest numbers (Fig. 2) and the reduction of grass biomass caused by grazing, which means fires cannot progress.

Rainfall occurs largely from November to June, there being a gradient of high annual rainfall (1200 mm) in the northwest to semidesert conditions (500 mm) on the plains in the southeast (Norton-Griffiths et al. 1975). This rainfall gradient influenced movement patterns, with

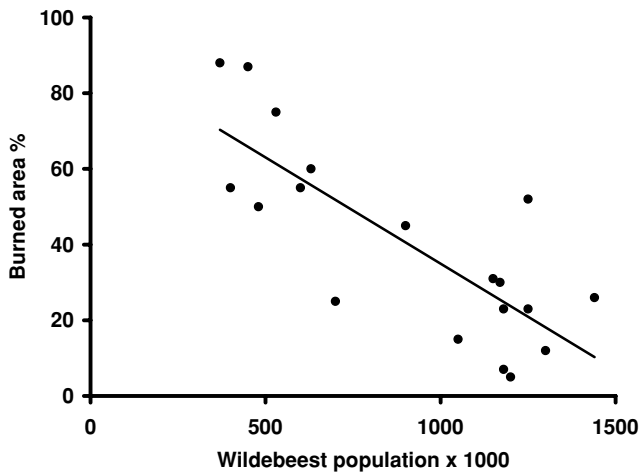


Figure 2. The area of the Serengeti woodlands burned in grass fires relative to wildebeest numbers. Burn data are from aerial surveys (Norton-Griffiths 1979; A.R.E.S., unpublished), and wildebeest numbers are interpolated from Fig. 1.

wildebeest moving to the northwest as the dry season progressed (Maddock 1979). Anomalously high rainfall in the dry months resulted in migration reversing and animals appearing on the plains, as in August 1971 (Maddock 1979).

Evidence for long-term trends in rainfall are equivocal. The longest record (1902–1991), at Musoma on Lake Victoria just west of Serengeti, shows a steady increase. Nevertheless, the longest record within the ecosystem (1938–2002), at Banagi and the central woodlands, shows no trend. There is an indication of a 10-year periodicity of low rainfall years, but this is not yet significant. In southern Africa this decadal oscillation is more pronounced (Vines 1980).

In Serengeti the extreme seasons have provided the most information on system dynamics. Over the past 50 years there have been two high rainfall years (1961–1962 and 1997–1998) and three severe drought years (1960, 1984, 1993). There is relatively little information on events in the early 1960s. The floods of 1961 may have been instrumental in reducing lion populations through disease (C. Packer, personal communication), and the high rainfall did not improve survival of wildebeest calves because of the overriding effect of rinderpest that was still present. In contrast the floods of 1997–1998 improved calf survival in many ungulate species, including wildebeest (A.R.E.S., unpublished data). Several bird species, particularly those nesting in tallgrass, such as Helmeted Guineafowl (*Numida meleagris richenowi*) and White-browed Coucal (*Centropus superciliosus*), showed marked peaks in numbers (A.R.E.S., unpublished data).

The drought of 1984 caused substantial mortality in buffalo, especially in the MMNR (some 40% of the popu-

lation; H. Dublin, personal communication). The drought of 1993 was even more severe and caused 40% mortality of wildebeest and 70% mortality of buffalo through starvation. The subsequent increase of the wildebeest population to its previous level provided confirmation of the food regulation hypothesis (Hilborn & Sinclair 1979; Sinclair et al. 1985; Mduma et al. 1999). In general the long-term records have allowed us to utilize infrequent abiotic perturbations to understand natural regulatory processes in the system.

These records also show that biotic processes can modify abiotic effects because wildebeest grazing has altered the extent of burning, the opposite of the typical interpretation of linkages. Conventionally, linkages were understood to be unidirectional; that is, the biotic realm is built on a foundation of preset abiotic processes. These observations on the bidirectional linkage between biotic (grazing) and abiotic (fire) processes have increased our understanding of ecosystem processes.

The Role of Elephants in Multiple Ecosystem States

In the 1960s elephants were regarded as the culprits of the decline of mature woodlands throughout savanna Africa because elephants were seen pushing over trees. At the time there were general calls for culling of elephants (Lamprey et al. 1967; Laws 1969; Laws et al. 1975).

In the Serengeti there were simultaneous studies being conducted on the effects of fire on woodland demography (Glover 1968). Norton-Griffiths (1979) concluded that fires effectively limit recruitment of young trees and that the extent of burning in the dry season has to be <30% of the woodlands if recruitment is to balance adult mortality, most of which was due to senescence rather than elephants. In reality the extent of burning was near 80% in the mid 1960s, demonstrating that the collapse of the *Acacia* tree populations, which occurred largely in that decade (Dublin 1995), was due to an exceptionally high incidence of burning.

Nevertheless, the extent of burning declined to a minimum in 1980 and has remained relatively low subsequently because of heavy grazing by wildebeest. Areas burned since 1980 have been between 5% and 25%, indicating that significant recruitment of trees should have occurred. In the MMNR burning was around 5% in the early 1980s, but tree recruitment was absent. Dublin (1986) showed that elephants ate young tree recruits so extensively that no recruitment took place. These studies demonstrate that ecosystems can occur naturally in more than one combination of species populations; that is, there are multiple ecosystem states, in this case a woodland state and a grassland state both with elephants. A disturbance such as fire is required to change the state from woodland to

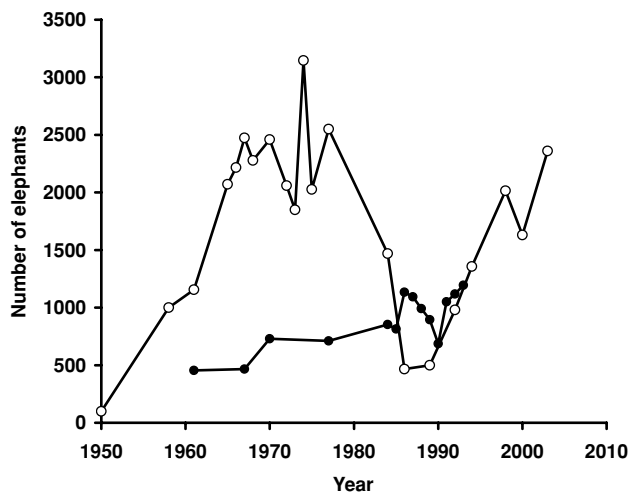


Figure 3. Elephant numbers in the Serengeti woodlands (open circles) and Mara Reserve (closed circles) from 1950 through 2003. Data from Dublin and Douglas-Hamilton (1987) and A.R.E.S., S.A.R.M., and H. Dublin (unpublished reports).

grassland, but once grassland occurs elephants can keep it in that state (Dublin et al. 1990b; Sinclair 1995a).

To test the concept of multiple ecosystem states, fire and elephant numbers need to be reduced so that woodlands can regenerate. These conditions occurred in the Serengeti part of the ecosystem during the 1980s when some 84% of the elephants disappeared either because of poaching (about 2000 animals) or emigration to the MMNR (about 300 animals). In contrast, in the MMNR elephant numbers were relatively constant at about 800 up to the mid 1980s, when the population increased to around 1100 because of this movement (Fig. 3).

Photographs have been taken from the top of hills or kopjes in locations throughout the Serengeti woodlands to monitor tree densities, starting in 1980 and continuing at intervals since then. In addition, some photographs of sites taken in previous decades were discovered, and new pictures of these sites were taken. Densities of mature trees declined prior to 1980, but then there was a sudden, sharp increase (Fig. 4). This result confirms the prediction that both the reduction in burning caused by wildebeest grazing and the reduction of elephant browsing on seedlings are necessary to restore the woodlands. Our understanding of these interactions, however, was derived from examination of effects of disturbances (often unpredictable) of known causes over many decades.

Indirect Interactions: the Role of Predators

Whereas food supply limits the migrant population of wildebeests and large species of resident ungulates, infor-

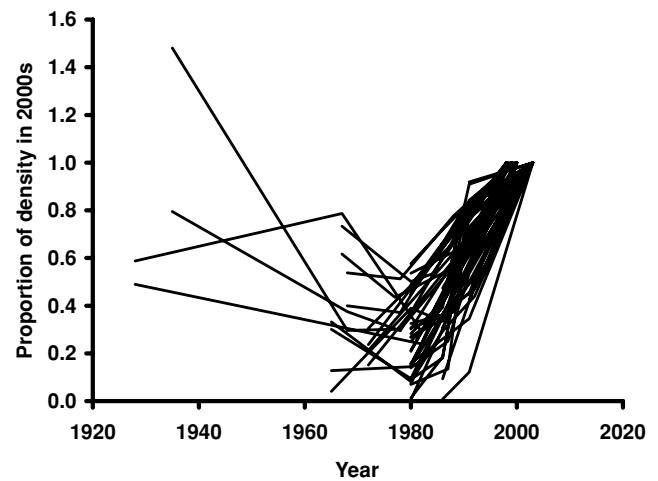


Figure 4. Tree densities based on photographs taken at various dates back to the 1920s relative to tree densities from photographs taken in the 2000s. Data from Sinclair (1995a) and A.R.E.S. (unpublished).

mation on causes of mortality in adults of smaller resident ungulates shows that they are limited by predation (Sinclair et al. 2003). Smaller ungulates are exposed to many more species of carnivore and so suffer higher predation. In contrast, predators cannot kill very large adult ungulates. There is a threshold of prey size where the main mode of limitation switches rapidly from that caused by food to that caused by predators as prey become smaller. This threshold body weight, about 150 kg, is approximately that of wildebeest. Our data show that when wildebeest become sedentary as in western Serengeti, they become limited by predation (Sinclair et al. 2003). Migration, therefore, allows populations to escape predator limitation (Fryxell et al. 1988).

Lion (*Panthera leo*) populations on the Serengeti plains and adjacent woodlands have been monitored since the 1960s (Schaller 1972; Hanby & Bygott 1979; Whitman & Packer 2005 and references therein). In essence, the lion populations in both habitats increased. In particular, there has been an increase of lions in the woodlands since the 1980s, whereas wildebeest numbers have remained constant.

Recent studies (Hopcraft et al. 2005) demonstrate that lions' hunting success, their functional response to prey populations, is determined by the availability of dense cover for ambush rather than by the density of prey. These studies predict that the increase in dense cover due to the increase in young tree populations has benefited lions by enabling them to catch more prey; and greater hunting success should yield a decline in prey numbers. Population data indicate there has been a decline in most species of small- and medium-sized resident antelopes in the same area of the eastern woodlands. Similar trends are apparent in other areas, but lion numbers are not available. Figure 5

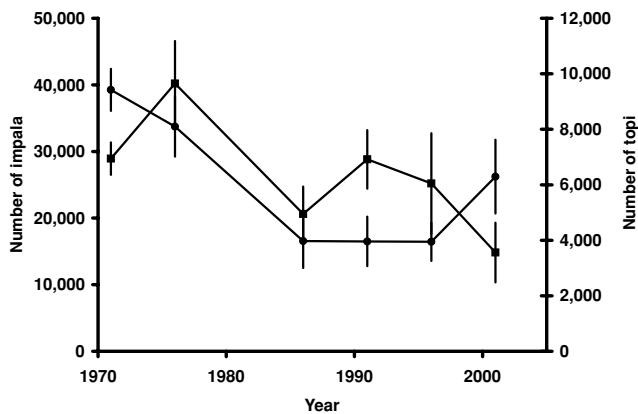


Figure 5. Numbers of topi (circles) and impala (squares) in the central and eastern woodlands from 1970 through 2000 (vertical bars, ± 1 SE). Data from Sinclair (1995b), Campbell and Borner (1995), and S.A.R.M. (unpublished).

illustrates the trend for two such species, topi (*Damaliscus korrigum*) and impala (*Aepyceros melampus*), since 1971. The downward trend has been most pronounced since 1980, which covers the period when there was a substantial increase of young trees. Thus, plant structure indirectly affects predator functional responses and thereby herbivore numbers.

Slow Change in Woodland Communities

Slow change in a system becomes apparent only when one has both an initial baseline of data and sufficient long-term monitoring to detect the change. In the Serengeti, woodland plant communities have been observed over several decades through aerial photography, photopoints from set locations, and assessments of age (Dublin 1986; Dublin et al. 1990b; Sinclair 1995a; Packer et al. 2005). In the past 120 years there have been two periods of pulsed recruitment of seedlings: an early cohort of trees that originated in about 1890 with the rinderpest panzootic described above and a cohort that originated in the late 1970s with the increase of wildebeest (Fig. 4 and Sinclair 1995a). These observations also show that in parts of the ecosystem the tree species that dominated the woodlands changed. Before the 1960s the woodlands of central and southern Serengeti were dominated by *Acacia robusta* Burch. (= *A. clavigera* E. Mey. ssp. *usambaren-sis*) and *Commiphora* species. Nevertheless, in the 1960s and 1970s these species declined and *A. bockii* De Wild., and *A. senegal* (L.) Willd. dominated the community (Herlocker 1976). Since the early 1980s, *A. robusta* has been regenerating and now (2000s) has regained dominance, whereas *Commiphora* is beginning to reappear.

Several sites in the Serengeti have monospecific stands of the small whistling thorn tree (*A. drepanolobium* Sjosted). These stands have gone through a cycle of senescence and regeneration. In 1965 they occurred as mature stands. By 1980 they had largely died out and wet grassland remained. By 1990 they were regenerating in dense stands of trees <1 m high; by 2000 they were back to a mature height of 3–4 m.

Savanna trees in Serengeti have regenerated in pulses of even-aged stands typical of other savannas in Africa and Australia. The changes we describe for *A. drepanolobium* and *A. robusta* communities have also occurred in most of the *Acacias* (e.g., *A. polyacantha* Willd. ssp. *campylacantha*; *A. gerrardii* Benth. var. *calvescens* Brennan; *A. tortilis* [Forsk.] Hayne ssp. *spirocarpa*; *A. senegal*, *A. seyal* Del. var. *fistula* [Schweinf] Oliv.) and other woodland types such as *Terminalia* and *Commiphora*. These changes have been synchronized over the whole Serengeti ecosystem (A.R.E.S., unpublished data). The cycle of savanna community composition, with associated birds and insects, has a period of about 30–40 years for the smaller trees and closer to 80 years for the larger trees such as *A. robusta* (Sinclair 1995a, Sinclair et al., in press).

The Role of Wildebeest as a Keystone Species

Wildebeest affect the populations and communities of species far beyond their immediate food or predator species. We have evidence that they maintain the diverse assemblage of small herbaceous flowering plants on the plains—removal of grazing for a decade changes the shortgrass plains into tallgrass communities (A.R.E.S., unpublished data). With this change of grass structure there are changes in grasshopper diversity—some 49 species occur in tallgrass, whereas fewer than 13 species occur in shortgrass. As the wildebeest population has increased, plant species diversity has declined (A.R.E.S., unpublished data). Similarly, grassland structure determines the types of bird species that occur in the grassland, particularly among ground-living larks, pipits, and wheatears (Sinclair 2003; A.R.E.S., unpublished data). The conclusion that wildebeest affect most components of an ecosystem derives from the consequences of the increase of the population in the 1960s and 1970s. The implication is that loss of the wildebeest migration would radically alter the ecosystem.

Direct and Indirect Impacts of Anthropogenic Disturbances

Long-term monitoring has highlighted several impacts of humans on the ecology of the Serengeti. Following the

eradication of rinderpest, buffalo numbers increased in parallel with wildebeest until 1976 (Figs. 1a–b). There followed a precipitous decline over the next 20 years that has been due largely to illegal hunting by humans (Dublin et al. 1990a; Campbell & Hofer 1995; S.M., unpublished data). The increase in hunting arose from the political turmoil following the border closure between Tanzania and Kenya in 1977. Tourism revenue dropped by about 90% and antipoaching activities ceased for more than a decade (Sinclair 1995c). Most of the decline took place in areas close to human populations, particularly in northwestern Serengeti, where the initial high density of buffalo effectively was reduced to zero. Continued human interference in northwestern Serengeti is now preventing buffalo numbers from recovering, whereas in eastern areas, remote from high human density, numbers are beginning to recover (Hilborn et al. 2006).

There are also indirect effects of humans on the protected area. For example, the rapidly increasing immigration of humans surrounding the natural ecosystem (Kurji 1976 in Norton-Griffiths 1979; Campbell & Hofer 1995) has caused an influx of domestic dogs (some 30,000 are thought to be surrounding the ecosystem [S. Cleveland, personal communication]). These dogs have transferred canine distemper to wild carnivores, precipitating epizootics and high mortality (Roelke-Parker et al. 1996; Packer et al. 1999; Cleveland et al. 2000). The direct and indirect effects of humans on this ecosystem were detected only because there were prior baseline data with which to make a comparison. In addition, long-term data are necessary to detect slow changes in the system, such as changes in disease prevalence, which may be imperceptible in the short term.

A recent suggestion is that reserves act as genetic refuges that counteract selection changes imposed by human harvesting. There have been noticeable trends, for example, in the proportion of tuskless elephants in Zambia. This proportion increased from 11% to 38% in only 20 years, purportedly due to the selection of large tusks by hunters (Jachmann et al. 1995). Models that explore the rate of decline in allele frequencies show that population declines are considerably less if a segment of a population, in this case kangaroos in Australia, is protected from harvesting (Tenhumberg et al. 2004).

Natural Areas as Ecological Baselines

Slow change is often difficult to detect when one is a part of it. Thus, baselines that exclude (or at least reduce) the impact of humans, as in protected areas, play a vital role in highlighting the negative impacts of humans on their own ecosystem (Sinclair 1998). For example, we compared the species diversity of insectivorous and granivorous birds in natural savanna woodlands with that in the immediately

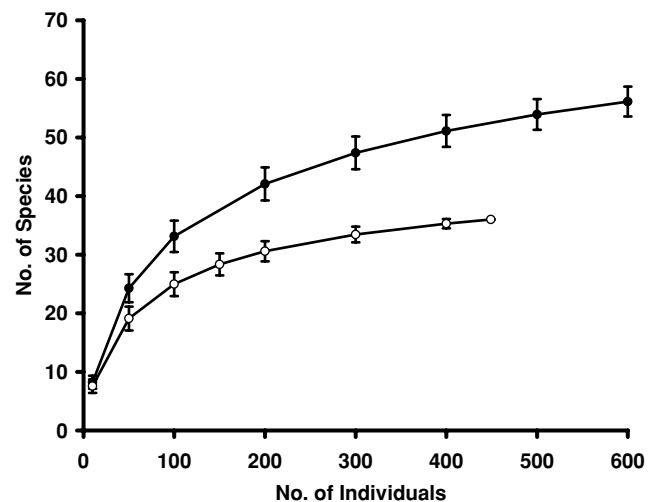


Figure 6. Rarefaction curves for species richness of insectivorous and granivorous birds in savanna woodlands of Serengeti (solid circles) and adjacent smallholding agriculture (open circles) (vertical bars, ± 1 SD). Data from Sinclair et al. (2002).

adjacent smallholding agriculture with rarefaction analysis (Krebs 1999; Fig. 6). Some 50% of the species dropped out of agricultural landscapes, and some 80% of the density of the remaining species was lost. These losses are due to a combination of changes in habitat structure (loss of trees) and reduced insect food supply (not lost due to pesticides; Sinclair et al. 2002). It is known that the agricultural areas in northwestern Serengeti were still natural savanna some 50 years ago; thus, these losses have taken place since then. If such losses are typical in agricultural landscapes in East Africa, then much of the African savanna avifauna will become confined to protected areas in the next few decades. This raises the issue of whether the protected areas are large enough to support species that are not adapted to extreme fragmentation. This issue urgently requires further study in Africa.

One of the important lessons coming out of long-term monitoring is that ecosystems are always changing. One implication that concerns conservation is that short-term data sets that show rapid declines in population can result in a species becoming listed as endangered when the trend is extrapolated to extinction within, say, 100 years. Then the trend turns around and the risk of extinction declines. Such short-term fluctuations might obscure longer-term downward trends. Without the longer time series one does not know how to interpret the short-term trends. In general, we suggest that more emphasis be placed on reconstructing data back in time. One could use, for example, past photographic records as in the present example, pollen cores, ice-cores, and other paleontological data so as to understand natural variation on a broader scale.

Effects of History

The structure and dynamics of an ecosystem can exhibit the signature of events that took place many decades, sometimes hundreds of years previously, and it is important to bear this in mind when interpreting present day ecosystem dynamics. The Serengeti illustrates this point with two historical events. First, the effects of the Great Rinderpest some 120 years ago are still being felt today through indirect consequences on vegetation, herbivores, and predators.

Second, in the latter half of the 1800s, elephant populations in Africa as a whole declined principally due to the loss of habitat through cultivation in the colonial period (Milner-Gulland & Mace 1991; Milner-Gulland & Beddington 1993). In certain areas, however, elephants were exterminated well before the spread of cultivation. From 1840 to 1870 Arab traders from Zanzibar pushed progressively westward across East Africa in a search for ivory, which had rapidly increased in price. The traders supplied guns to local people who then systematically reduced elephant populations, first near the coast and then further inland, to supply the ivory caravans (Tippu Tip in Brode 1903; Spingale 1973).

One of the caravan routes went directly through Serengeti. Travelers describe that Wandorobo hunters lived in the central Serengeti woodlands, where they had neither farms nor livestock but existed entirely on ivory exports in the 1860s (Wakefield 1870). Elephant populations east and south of Lake Victoria had been decimated by the 1860s (Brode 1903), however. The explorer J.H. Speke observed that populations west of the lake were declining rapidly (Spingale 1973).

These events, which were characteristic of East Africa, shaped the vegetation in subsequent decades when explorers described the areas—an abundance of trees in many areas of East Africa, such as Tsavo National Park in the 1890s, was accompanied by a complete absence of elephants and no cultivation (Patterson 1907). Tsavo had previously been the hunting grounds for ivory-hunting tribes. The subsequent increase in elephants in protected areas in the 1950s (Fig. 3) was a sharp contrast to the rapid decline in elephant numbers over Africa as a whole, indicating a retreat to these areas from human disturbance outside. Thus, elephants and their interactions with trees (Laws et al. 1975) have to be viewed in the light of events more than a century earlier.

The Value of Long-Term Data for Conservation

Long-term studies, such as those in Serengeti, Kruger, and Yellowstone, usually begin for short-term eclectic reasons. Nevertheless, as they progress, new events lead to further research and the combined data lead to insights

that are then related to the time series. The definition of *long term* and the value of the length of time the data set covers are independent of the life history of the species concerned. We are as much interested in the effects of infrequent drought on soil microbes as we are on elephant populations. Thus, *long term* is a function of the slower variables (or slowest variable) in the system, in our case the events related to rainfall.

The complex ecosystem behavior involving slow and rapid change and multiple ecosystem states only became apparent over a period of several decades. Ecosystems are subject to long-term environmental events. Conservation needs to take into account infrequent and unpredictable events, such as floods, fire, and droughts. Long-term data are most necessary to measure the impacts of these events, such as the Serengeti floods 36 years apart and droughts 10–23 years apart. Long-term data are also required to measure slow trends due to environmental change, plant succession, and animal population fluctuation. These slow trends show an interaction between abiotic and biotic processes, each affecting the other, as illustrated by changes in grazing pressure reducing the extent of burning. The long-term changes observed here highlight the point that ecosystems are not static. Therefore, management should not aim to maintain the status quo; rather, it should allow natural change to take place. In protected areas, however, changes due to direct human impacts may need to be counteracted through management action. In general, long-term baseline data are fundamental to conservation and management because they provide the background to interpret causes of change and hence determine the course of conservation.

Natural and anthropogenic disturbances provided insight into mechanisms of ecosystem regulation and stability, in this case to understanding wildebeest population dynamics and the role of predators in limiting the smaller-sized resident ungulates. Disturbances from human hunting were also instrumental in our understanding of multiple states.

Linear indirect effects, or cascades, have become apparent from the present studies of wildebeest as a keystone species. Nonlinear indirect effects between trophic levels were detected in changes of vegetative cover, which indirectly affected herbivores through their predators.

Slow change can become an irreversible and rapid shift into a new state in which the system can remain for long periods, perhaps until a new disturbance shifts it to a new state or back to the original state. This was observed in the interaction of grasslands, woodlands, and elephants. The gradual decline in canopy cover from the 1920s become rapid in the 1960s; conversely, tree recruitment was very low for decades before the rapid pulse of the 1980s and 1990s. Where elephants were at sufficient density, the system was locked into a grassland state, whereas before burning it was a woodland system. Thus, conservation managers need to consider that the ecosystem can occur

in multiple states. Some of these can be natural, but others can be artifacts of anthropogenic or other disturbances.

Ecosystems should be managed at an appropriate spatial scale. Small patches of forest are insufficient to support viable populations of, for example, animals within patches of riverine gallery forest. Large areas are required for migrating ungulates that move between wet-season and dry-season range (Thirgood et al. 2004). Sufficient area is required to produce the mosaic of burns and grazing disturbances important for the habitat heterogeneity that can be used as sources and sinks for animal populations. The time scales of both unpredictable, sudden events and slow change dictate the time scale for conservation planning. In this case planning must be for 30- to 50-year periods or longer.

Conservation efforts outside protected areas must distinguish natural change from direct, human-induced change. To do this protected areas are essential because they act as the ecological baseline where human-induced change is kept to a minimum. Long-term data are required to make this distinction. Management within protected areas is then designed to mitigate human disturbances. In Serengeti poaching and disease transfer are examples of such disturbances. Protected ecosystems can then be compared with human ecosystems to detect the human impacts that are occurring slowly (e.g., the decline in avifauna west of Serengeti).

How should these lessons on ecosystem dynamics, obtained from nearly 50 years of study, be taken up by management? The most important need is the transfer of information to managers, and this requires close and frequent communication between researchers and managers. Second, researchers need to inform managers of new findings, particularly of a shift in perspective due to the new findings. For example, in the 1960s the disappearance of trees in Serengeti was perceived to be due to elephant destruction, but as the work on both elephants and fire proceeded it was realized that fire was the driving factor and management had to change its emphasis toward fire management. Third, researchers need to highlight trends or events that could lead to conservation problems in the future—they should provide an early warning of possible problems. Thus, the precipitous decline in buffalo numbers, detected by 1984, led to advice being given to management on the effects of human intrusions. Fourth, managers should inform researchers of their priorities in conservation and their perception of management problems. These perceptions may or may not be real, but that is for the researchers to establish. For example, current conservation priorities in Serengeti involve the protection and expansion of the black rhinoceros (*Diceros bicornis*) population that was almost eradicated in the 1970s. Other priorities include the impacts of wildlife—particularly the increasing elephant population—on the human population on the western boundaries of the park. Researchers need to focus on facilitating or ameliorating these issues

as short-term goals without losing sight of the long-term trends. These four needs require a working group of researchers and managers. Although this has not been set up in a formal way, de facto communication has been developing well in recent years and cooperation is improving.

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